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Cultus Lake Sockeye Population Viability Analysis

Analyse de la viabilité de la population de saumons rouges du Cultus Lake

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ABSTRACT

A stochastic simulation model was developed to evaluate the efficacy of alternate captive broodstock programs, harvest rates, and freshwater habitat enhancement to recover the Cultus Lake sockeye population. The model simulates the abundance of emigrating smolts and returning adults based on a spawner-to-smolt stock-recruitment model and density-independent marine survival and pre-spawn mortality rates. The model accounts for removals of spawners for broodstock collection, and tracks the abundance of hatchery-produced smolts and returns as well as the production from hatchery-origin fish that spawn in the wild. The simulated numbers of both wild and naturally produced progeny from hatchery-origin spawners are compared to the recovery goals defined in the Cultus Lake Sockeye Recovery Strategy.

There was little information in the spawner-to-smolt data concerning depensatory mortality or density dependence. A depensatory model fit using prior information on carrying capacity based on Shortreed et al.'s (2001) euphotic volume model was consistent with error assumptions and eliminated over prediction of smolt numbers at low stock size that was apparent when using a standard Ricker stock-recruitment model. With termination of captive broodstock collection in 2007, the probability of meeting recovery objectives declined with increasing harvest rate and there were very large differences in performance between pessimistic and optimistic marine survival-pre spawn mortality (PSM) scenarios. Extinction probability increased substantially under higher harvest rates and was very sensitive to the assumed marine survival-PSM scenario. Under a limited set of conditions, continuation of the hatchery program or habitat enhancement improved recovery statistics and reduced the risk of extinction. Performance measures were very sensitive to the assumption of depensation in freshwater survival rate. Population recovery was best under a combined policy, which included reduction in harvest rate, continuous habitat enhancement, and extension of a hatchery supplementation program with a doubling in smolt capacity through 2015. As for any population viability analysis, the results presented here should be viewed with healthy skepticism. However, the modeling exercise was useful for examining the relative benefits of alternate recovery options, and for highlighting priorities for data collection and research.

RÉSUMÉ

Un modèle de simulation stochastique a été élaboré pour évaluer l'efficacité des programmes de rechange de cheptels géniteurs, les taux de récolte et l'amélioration de l'habitat dulcicole afin de rétablir la population de saumons rouges du Cultus Lake. Le modèle permet de simuler l'abondance de saumoneaux qui émigrent et d'adultes qui sont de retour selon un modèle stock-recrutement de géniteur à saumoneau, de même que selon les taux de survie en mer indépendants de la densité et les taux de mortalité avant le frai. Le modèle tient compte du retrait des géniteurs pour la population du cheptel et permet d'effectuer le suivi de l'abondance de saumoneaux d'élevage et des saumons qui sont de retour ainsi que de la production de poissons d'élevage qui ont frayé à l'état sauvage. Les quantités de descendance simulées provenant de la reproduction naturelle à l'état sauvage à partir de géniteurs issus d'écloserie sont comparées aux objectifs de rétablissement définis dans la Stratégie de rétablissement du saumon rouge de Cultus Lake.

Les données sur le rapport géniteur au saumoneau comportaient très peu de renseignements sur la mortalité dépensatoire ou la dépendance à la densité. Un modèle dépensatoire convenait en faisant appel à des renseignements préalables sur la capacité de charge fondée sur le modèle de volume euphotique établi dans l'étude de Shortreed et *al.* (2001) et correspondait aux hypothèses sur les erreurs, mais ce modèle dépensatoire ne tenait plus par rapport à la prédiction sur les quantités de saumoneaux en fonction de la faible taille du stock que l'on constatait selon un modèle stock-recrutement standard de Ricker. Comme la collecte de géniteurs pour le cheptel s'est achevée en 2007, la probabilité d'atteinte des objectifs de rétablissement s'est affaiblie en raison de l'augmentation des taux de récolte. On constatait aussi des différences de rendement fort importantes entre les scénarios pessimistes et optimistes de survie en mer/mortalité avant le frai. La probabilité d'extinction s'est accrue considérablement en raison des taux de récolte élevés et dépendait fortement du scénario hypothétique de survie en mer/mortalité avant le frai. Selon un ensemble restreint de conditions, la poursuite du programme d'écloserie ou d'amélioration de l'habitat a permis d'améliorer les statistiques de rétablissement et de réduire le risque d'extinction. Les mesures du rendement dépendaient fortement de l'hypothèse sur le taux de survie des populations en eau douce. Le rétablissement de la population était optimal en fonction d'une politique combinée qui prévoyait la réduction du taux de récolte, l'amélioration continue de l'habitat et la prolongation du programme d'agrandissement des écloseries en doublant la capacité en saumoneaux jusqu'en 2015. Comme pour toute analyse de viabilité d'une population donnée, les résultats présentés devraient être considérés avec un certain recul. Cependant, l'exercice de modélisation s'est avéré utile pour examiner les avantages de chacune des options de rechange en matière de rétablissement, de même que pour faire ressortir les priorités au chapitre de la collecte de données et de la recherche.

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1.0 INTRODUCTION

A stochastic simulation model was developed to conduct a population viability analysis (PVA) for the Cultus Lake sockeye salmon population. The main intent of the analysis and model was to evaluate the efficacy of alternate captive broodstock programs, harvest rates, and freshwater habitat enhancement actions to aid population recovery. The model simulates the abundance of emigrating smolts and returning adults based on a spawner-to-smolt stock-recruitment model and density-independent marine survival and pre-spawn mortality rates. Random variation in smolt production, marine survival rate, age-at-return, forecast error of pre-fishery recruits, and pre-spawn mortality is simulated. The model accounts for removals of spawners for broodstock collection, and tracks the abundance of hatchery-produced smolts and returns as well as the production from hatchery-origin fish that spawn in the wild. The simulated number of wild and naturally produced progeny from hatchery-origin spawners are compared to the recovery goals defined in the Cultus Lake Sockeye Recovery Strategy (Cultus Sockeye Recovery Team 2004). This report describes the structure of the model, summarizes the supporting data analysis used to parameterize it, and presents the main findings based on the current model structure and parameterization.

The Cultus Lake sockeye population viability model is one of the tools that has, and likely will be used, to evaluate alternate harvest regimes for the Fraser River Late run sockeye aggregate. Preliminary results from the model were used in a formal decision-making process in the spring and summer of 2006 as part of the Fraser River Sockeye Spawning Initiative and pilot Wild Salmon Policy implementation effort. Results presented in this report are used to describe the behaviour of the model only and are not intended to rank alternate harvest policies. Such a ranking needs to explicitly consider the effects of recovery actions on the Cultus population as well as all other late-run populations and fisheries, and therefore needs to be made in a broader planning context.

2.0 MODEL STRUCTURE

A two-stage life history model is used to simulate the numbers of outmigrating smolts and returning adult sockeye. The first stage predicts the number of smolts as a function of the number of spawners. The second stage predicts the number of pre-fishery recruits, spawners at the weir, and effective spawners reaching the spawning grounds based on the number of smolts, marine survival, harvest, and pre-spawn mortality rates (Fig. 1). The model tracks the abundance of the 3 stock types resulting from wild and hatchery production:

- The 'Wild' stock type (st='W') consists of fish that meet the requirements for wild fish as defined in the Wild Salmon policy (DFO 2004). Wild fish must be the progeny of parents that spent their entire life cycle in the wild.
- The 'Hatchery' stock type consists of fish that were released from the hatchery and are assumed to all have adipose clips (st='H').

- The 'Unclipped' stock type consists of fish that are first-generation progeny of the Hatchery stock type that spawned in the wild (st='U'). These fish are not considered wild salmon but not have an adipose clip.

Simulation structure for wild and unclipped stock types, and for the hatchery stock type, is described in Sections 2.1 and 2.2, respectively. See Tables 1, 4, and 5 for definitions of model indices, state variables, and parameters.

2.1 WILD AND UNCLIPPED STOCK SIMULATION

The number of wild and unclipped smolts exiting Cultus Lake is predicted from a Ricker stock-recruitment model with depensatory mortality using the equation:

$$(1) \qquad Sm_{st,t} = p_{st,t-i} E \frac{Sp_{T,t-i}}{Sp_{T,t-i} + \delta E_d} Sp_{T,t-i} e^{\alpha - \beta Sp_{T,t-i}} e^{u_t}$$

where, $Sm_{st,t}$ are the number of smolts leaving the lake in year t of stock type st (st='W' or 'U' only), $Sp_{T,t-i}$ are the total number of fish spawning i years earlier (effective spawners) for all stock types (which includes $Sp_{H,t-i}$), $p_{st,t-i}$ is the proportion of effective spawners made up of the hatchery, or wild and unclipped stock types, E is a multiplier used to simulate an improvement in freshwater habitat (that results in a proportional increase of E of number of smolts produced at any spawner level), E_d is a multiplier that simulates enhancement measures that reduce the magnitude of depensation, α, β, and δ are parameters of the stock-recruitment relationship for natural reproduction, and u_t represents annual deviations (process error) around the stock-recruitment curve which are assumed to come from a normal distribution with a mean of 0 and a standard deviation [illegible].

We assume that all juveniles leave the lake in the spring after spending 1.5 years in freshwater from egg fertilization (i=2). The $\frac{Sp_{T,t-i}}{Sp_{T,t-i} + \delta}$ term simulates the effects of depensatory mortality (Type II model of Barrowman et al. 2003). The parameter δ controls the extent of the depensation and is the number of effective spawners needed to reduce the expected number of recruits by 50% relative to a model without depensation. In the case when δ=0 (no depensation), e^{α} represents freshwater stock productivity (i.e., maximum smolts/spawner if [illegible]=0) and $1/\beta$ is the spawning stock size at which smolt production is maximized (sometimes referred to as S_{opt} or carrying capacity if [illegible]=0). The $p_{st,t-i}$ value used to predict the number of wild smolts is actually the sum of $p_{U,t-i}$ ($\frac{Sp_{U,t-i}}{Sp_{T,t-i}}$) and $p_{W,t-i}$ ($\frac{Sp_{W,t-i}}{Sp_{T,t-i}}$) since progeny of unclipped fish are classified as wild. This is where the transition between Unclipped and Wild stock types occurs.

A Bayesian approach is used to simulate stochastic variability in smolt production. A random record that specifies α, β, [illegible], and δ is drawn from the joint posterior distribution of parameter values for each simulation trial (see Section 2.5.1). For any year within that trial, mean smolt production will be determined by [illegible], and [illegible] and the simulated number of effective spawners. This mean value is then multiplied by a log-normal error term which is randomly determined each year and depends on the trial-specific value of [illegible]. The prediction of the number of hatchery-origin smolts leaving the lake in year t ($Sm_{H,t}$) is described in Section 2.2.

The number of pre-fishery recruits is predicted from:

$$R_{st,t} = \sum_{j=4}^{5} Sm_{st,t-j+2}\, pa_{N,j}\, MS_{t-j}\, \phi_{st} \quad (2)$$

where, $R_{st,t}$ is the number of adult recruits in year t of stock type st, $pa_{N,j}$ is the proportion of adults returning j years after spawning for fish that spawned in the wild (N for natural spawning), MS_{t-2} is the marine survival rate for this cohort of fish, and ϕ_{st} is the relative survival rate for hatchery and unclipped stock types compared to the rate for wild fish (i.e., $\phi_W=1$, $\phi_H \leq 1$, $\phi_U \leq 1$). $pa_{N,4}$ and $pa_{N,5}$ represent the proportion of 4 and 5 yr old returning spawners, respectively. Jack (age 3 at return) and age 6 returns are negligible for the Cultus stock and are not simulated. $pa_{N,4}$ is a stochastic variable predicted from a normal distribution with mean μ_a and standard deviation σ_a ($pa_{N,4}$=Norm(μ_a, σ_a)) and $pa_{N,5}$=1-$pa_{N,4}$. The mean and standard deviation of for the proportion at age 4 computed in logit space and stochastic values returned from the normal distribution are then backtransformed into linear space. This ensures that stochastic deviation in age-at-maturity always falls between 0 and 1.

Marine survival rate is predicted from:

$$MS_t = \overline{\mu_{ms}} e^{\omega_t - \frac{\sigma_{ms}^2}{2}} \quad (3)$$

where $\overline{\mu_{ms}}$ is the assumed mean survival rate and $e^{\omega_t - \frac{\sigma_{ms}^2}{2}}$ is a lognormal error term with bias correction. ω_t is a deviate drawn from a normal distribution with autocorrelated error and is predicted from:

$$\omega_t = \omega_{t-1}\rho_{ms} + \varepsilon\sqrt{1-\rho_{ms}^2} \quad (4)$$

where ρ_{ms} is the lag-1 autocorrelation coefficient in marine survival rate and ε is a normally distributed random variable with mean 0 and standard deviation σ_{ms} (i.e., $\varepsilon = N(0, \sigma_{ms})$).

The number of spawners reaching the weir is predicted from:

$$Esc_{st,t} = R_t - C_t \quad (5)$$

where, $Esc_{st,t}$ is the escapement at the weir in year t for stock type st, and C_t is the catch of Cultus returns. Catch of Cultus Lake sockeye is calculated as the product of the pre-fishery recruitment and a pre-determined annual harvest rate based on the Fraser River late-run aggregate (from FRSSI model), or based on harvest policies defined in the model. For the latter case, a modification of the harvest rate rule developed by Hilborn and Walters (1992) is used:

$$C_t = -E_{min} + h * \hat{R}_t \quad (6)$$

where, C_t is the desired total catch, E_{min} is the recruitment forecast below which no fishing occurs (the escapement floor), h is the slope and is equivalent to the harvest rate if there is no escapement floor (i.e., E_{min}=0), and $\hat{R}_t$ is the recruitment forecast. Parameters E_{min} and h can be adjusted to obtain a wide range of harvest strategies including:

1. constant harvest rate (E_{min}=0, h = desired harvest rate)
2. constant escapement (E_{min} = escapement target, h=1)
3. constant catch (E_{min} = -catch target, h=0)
4. floor policies where there is no catch below a minimum amount of recruitment, but as the total return increases, so does the catch (E_{min} =escapement target, 0<h<1).

As well, catch is constrained so that the exploitation rate does not exceed a maximum cap ER_{cap} (i.e., $\frac{C}{\hat{R}_t} \leq ER_{cap}$) or is less than zero. $\hat{R}_t$ is predicted as the sum of recruitment across all stock types (eqn. 2) and a bias-corrected lognormal observation error term representing the uncertainty in pre-fishery recruitment predictions,

$$\hat{R}_t = \sum_{st=1}^{3} R_{st,t} e^{\tau - \frac{\sigma_{for}^2}{2}} \tag{7}$$

where, τ is a deviate drawn from a normal distribution with mean 0 and standard deviation σ_{for}. Note that because error in the recruitment forecast is simulated, the realized harvest rate will deviate from the target rate identified by the harvest rule. However, no additional error, such as that associated with determining the magnitude of the catch (to decide when to terminate harvest), is simulated. The model also does not simulate potential biases in harvest implementation, such as a tendency to exceed the catch quota.

The number of effective spawners is predicted from,

$$Sp_{st,t} = (Esc_{st,t} - Brood_{st,t}) * (1 - PSM_t) \tag{8}$$

where, $Sp_{st,t}$ is the number of effective spawners in year t for stock type st, $Brood_{st,t}$ is the number of fish at the weir taken for broodstock (see Section 2.2), and PSM_t is the pre-spawn mortality rate in year t. As for the marine survival rate, PSM_t is a stochastic variable with autocorrelated error predicted from eqn.'s 3 and 4, with parameters μ_{psm}, σ_{psm}, and ρ_{psm} replacing μ_{ms}, σ_{ms}, and ρ_{ms}, respectively. The total number of effective spawners used to predict smolt production in eqn. 1 is computed as the sum of effective spawners of each stock type,

$$Sp_{T,t} = Sp_{W,t} + Sp_{U,t} + Sp_{H,t} \tag{9}$$

An extinction rule is used to simulate demographic and genetic risks to population sustainability by setting $Sp_{T,t}$ to zero if $Sp_{T,t}$ is less than a fixed extinction limit.

2.2 HATCHERY STOCK SIMULATION

Simulating the production from the Cultus Lake hatchery requires considerable bookkeeping due to the complex nature of the operation (Fig. 2). Eggs taken from broodstock are used to produce unfed fry, fed fry, and smolts that are released into Cultus Lake. A small proportion of eggs from the original broodstock are reared to maturity in the hatchery to provide broodstock for production in the next generation. The vast majority of the captive broodstock mature at ages 3-5. The hatchery has limited capacity to produce fed fry and smolts and unfed and fed fry in excess of these capacities are released to the lake. Total numbers released to the lake will depend on the number of broodstock collected, survival rates in the hatchery, and carrying capacity for fry and smolts. Survival rates from egg to unfed fry are different for eggs collected from wild and captive broodstock. Survival from release to emigration past the Sweltzer

Ck. Fence as smolts varies by the life stage of release. Equations describing these dynamics are provided below.

The number of wild and unclipped spawners at the weir taken for broodstock is computed from,

$$Brood_{st,t} = \frac{Esc_{st,t}}{Esc_{U,t} + Esc_{W,t}} \min(h_H (Sp_{W,t} + Sp_{U,t}), MaxTake) \quad (10)$$

where, h_H is the maximum proportion of unclipped fish at the weir that can be taken for broodstock (the hatchery-induced harvest rate), and *MaxTake* is the maximum number that can be taken into the hatchery. This calculation harvests the total number of unclipped fish at a rate of h_H when the escapement of unclipped fish is less than *MaxTake*, and at a reduced above this value. If the brood take is less than the target *MaxTake*, the balance can be made up from hatchery-origin clipped fish up to the number of clipped fish that are present based on the equation,

$$Brood_{H,t} = \min(MaxTake - Brood_{W,t} - Brood_{U,t}, Esc_{H,t}) \quad (11)$$

Collection of clipped fish for broodstock must be specified by the user and is not the default model option.

The number of eggs collected for hatchery production each year ($TEggs_t$) is simply the product of the number of broodstock collected and the average sex ratio (sx) and fecundity (F),

$$TEggs_t = (Brood_{W,t} + Brood_{U,t} + Brood_{H,t}) * sx * F. \quad (12)$$

The number of eggs used to produce fry to be released into the lake the following year (SupEggs) is determined from,

$$SupEggs_t = TEggs_t - CBEggTake_t \quad (13)$$

where, $CBEggTake_t$ is the number of eggs required to produce 500 adult captive broodstock. To simulate a supplementation-type hatchery operation that does not rear captive broodstock $CBEggTake_t$ is set to 0. The number of eggs produced from captive broodstock is the sum of the total eggs produced from fish that mature at ages 3 to 5 in the hatchery,

$$CBEggs_t = \sum_{iage=3}^{5} EggsFromCB_{iage} \quad (14)$$

where, $EggsFromCB_{iage}$ is the total number of eggs produced from captive brood maturing at '*iage*'. This parameter is constant for each age of maturity and depends on the proportion of fish maturing at each age and their sex ratios and fecundities. $EggsFromCB_{iage}$ is not used in the sum calculation for $CBEggs_t$ in year '*t-iage*' when a captive brood-type hatchery operation is not simulated.

The total number of unfed fry produced in the hatchery is,

$$UFF_t = SupEggs_{t-1} * EUFsurv + CBEggs_{t-1} * CB\_EUFsurv \quad (15)$$

where UFF_t are the number of unfed fry, and *EUFsurv* and *CB_EUFsurv* are the egg-to-fry survival rates for eggs taken from wild and captive broodstock, respectively.

The number of unfed fry released into Cultus Lake (*UFLake*) is simply the excess relative the capacity of the hatchery to rear fed fry (*FryCap*),

(16) $$UFlake_t = \max(UFF_t - FryCap, 0)$$

The number of unfed fry remaining in the hatchery is simply UFF_t - $UFlake_t$.

The number of fed fry released into the lake (*FFlake*) is computed from

(17) $$FFlake_t = \max(UFF_t - UFFsmolt, 0) * UFFFFsurv$$

where, *UFFsmolt* is the number of unfed fry required to meet the hatcheries capacity to produce smolts (*SmoltCap*) and *UFFFFsurv* is the unfed fry to fed fry survival rate in the hatchery. UFFsmolt is a constant and is computed from $\frac{SmoltCap}{UFFFsurv * FFSMsurv}$

where, *FFSMsurv* is the survival rate from fed fry to smolts in the hatchery. The number of smolts released to the lake or below the fence is computed from,

(18) $$SMlake_t = (UFF_{t-1} - \frac{FFlake_{t-1}}{UFFFFsurv}) * UFFFFsurv * FFSMsurv$$

where the $\frac{FFlake_{t-1}}{UFFFFsurv}$ term is the number of unfed fry required to produce the number of fed fry released into the lake.

Finally, the total smolt production passing the fence is computed from,

(19)

$$SM_{H,t} = SMlake_t * LkSMsurv * E_{H,SM} + FFlake_{t-1} * LkFFSMsurv * E_{H,FF} + UFlake_{t-1} * LkUFSMsurv * E_{H,UF}$$

where, *LkSMsurv*, *LkFFSMsurv*, and *LkUFSMsurv* are the survival rates from release to migration past the fence as a smolt for fish released as smolts, fed fry, and unfed fry, respectively. $E_{H,SM}$, $E_{H,FF}$, and $E_{H,UF}$ are the relative improvements in the in-lake survival rates due to habitat enhancement for fish released as smolts, fed fry, and unfed fry, respectively. Note that $E_{H,x}$ values should be adjusted only when E and E_d values are also changed to simulate habitat enhancement. If hatchery smolts are released at the weir, $E_{H,SM}$ should be set to 1 as increases in in-lake productivity will not influence their survival rate. Also note that the product of $E_{H,x}$ and it's natural survival rate (e.g. LKUFSMsurv for $E_{H,UF}$) must not exceed 1.

2.3 MODEL PERFORMANCE

The effects of reduced harvest rates, enhanced freshwater productivity, and changes to the captive broodstock program were evaluated by computing a series of performance measures (PMs) based on the predicted number of effective spawners and recovery rules defined in the Cultus Lake Sockeye Recovery strategy (Bradford and Wood 2004, Table 2). Two sets of statistics were computed using both the number of true wild and the sum of true wild and

unclipped spawners (progeny of hatchery-origin parents that spawned in the wild). The set of statistics based on only wild spawners represents the performance according to the Wild Salmon policy. This statistic would be challenging to measure in practice, as the pedigree for fish passing the weir, and all fish released from the hatchery, would need to be determined. The second set of statistics, based on the total number of unclipped effective spawners, represents the performance that can be realistically assessed within the current financial constraints of the hatchery program. We used statistics based on unclipped spawners in this analysis.

2.4 MODEL INITIALIZATION

The total simulation period is 39 years from 1999 to 2037. The first 7 years, from 1999-2005, are initialization years. The remaining 32 years (8 generations), between 2006 and 2037, represent the simulation period over which performance measures are computed. Observed numbers of outmigrating smolts and effective spawners are used in place of simulated numbers for initialization years. The initialization period extends back to 1999 to compute recovery objective II for the first simulated year in 2006. The observed effective spawner numbers in the last few years of the initialization period are used in place of predicted spawners to compute the number of smolts via eqn. 1. The observed smolt production in the latter years of the initialization period are used to predict future recruits in place of using predicted smolt numbers. The number of hatchery-origin smolts counted at the Sweltzer Ck. fence are used to initialize the model prior to 2006. The number of unfed fry and the number of eggs from captive broodstock and wild fish in the hatchery are used to estimate hatchery production in 2006. Initial conditions are summarized in Table 3.

2.5 MODEL PARAMATERIZATION

Data used to parameterize the model natural production component of the model (Section 2.1) are provided in Appendix A (Table A1).

2.5.1 Spawner-to-Smolt Stock Recruitment Parameters

We estimated parameters of the spawner-to-smolt stock recruitment relationship by maximizing the log of the Bayesian probability of the parameters given the data. Our likelihood formulation assumes that error in predicted smolt numbers is log normally distributed. The log of the Bayesian probability is computed from,

$$Ln(P) = -\sum_{i=1}^{n} \frac{(\ln(Y)_i - Ln(\mu_i))^2}{2\sigma^2} + Lnp_0(P) \quad (20)$$

where, Ln(P) is the log of the Bayes posterior probability of parameters P (α, β, δ from eqn. 1 and the nuisance variance parameter σ), Y_i are the observed number of smolts in years 1 to n, μ_i is the predicted number based on the stock-recruitment parameters (α, β, δ), and $Lnp_0(P)$ and is the log of the prior probabilities on β and δ. The log prior probability is computed from,

$$Lnp_0(P) = -\frac{(Ln(\beta) - Ln(\mu_\beta))^2}{2\sigma_\beta^2} - \frac{(Ln(\delta) - Ln(\mu_\delta))^2}{2\sigma_\delta^2} \quad (21)$$

where, μ_β and σ_β are the mean and standard deviation of the normal prior distribution for the density dependent term, and μ_δ and σ_δ are the mean and standard deviation of a normal prior distribution for the depensation term. Note that in simulating smolt numbers from eqn. 1, there is no need to implement a bias correction term because the bias is already accounted for by logging predicted and observed recruits in the likelihood kernel.

Parameter estimates were computed assuming no prior information on any parameters ($Lnp_0(P)=0$), prior information on only density dependence, and prior information on both parameters (as in eqn. 20). We examined the influence of using prior information on the parameter estimates by comparing posterior distributions of stock-recruitment parameters assuming no prior information (uniform priors) and both informative (low values of σ_β=0.25 and σ_δ=0.25) and uninformative normal priors (high values of σ_β=0.5 and σ_δ=0.5). μ_β was assumed to be equal to $1/S_{opt}$, where S_{opt} is the number of effective spawners needed to attain the lake carrying capacity, as determined from the euphotic zone model of Shortreed et al. (2001) applied to Cultus Lake. We fit stock-recruitment models using all yrs. of available data (n=48, 1925-2003) and a subset of data (n=30, 1926-2001) where yrs. with predator removal, unclipped hatchery production, or yrs. with unknown pre-spawn mortality rates, were removed. This subset is identical to that presented in Figure 1 of Annex I of the Cultus Lake sockeye National Recovery Strategy (Cultus Lake Sockeye Recovery Team 2004) with the addition of the 2003 brood year.

In this analysis, we compare Ricker and depensatory stock-recruitment models only. We do not evaluate the Larkin stock-recruitment model, where carrying capacity parameters can vary by brood-cycle. A preliminary analysis (not shown here for brevity) revealed little difference in cycle-specific carrying capacity terms. Even if these terms had been substantially different, the results below show that there is not enough information in the dataset to estimate 4 separate carrying capacity parameters as well as productivity and depensation terms. Given the low abundance of the Cultus population, and that the depensation term will have a much greater influence on the PVA than the carrying capacity terms, it would make little sense to pursue the Larkin model in this context, even if the cycle-specific terms were substantively different.

The small sample size Akaike Information Criteria (AIC_c, Burnham and Anderson 2002) was used to compare Ricker and depensatory stock-recruitment models. AIC_c quantifies the tradeoff between model fit and complexity. AIC_c is computed as,

(22) $$AIC_c = -2\log(L(data|\hat{\theta})) + 2K\left[\frac{n}{n-K+1}\right]$$

The first term determines the model deviance computed at the maximum likelihood parameter estimates ($\hat{\theta}$ represents a vector of parameter values at their most likely estimates) and the second term represents model complexity based on the number of model parameters (K=3 or 4 for Ricker or depensatory models, respectively) and sample size (n=48 or 30 for full and smaller datasets, respectively). The model with the lowest AIC_c value is considered to have the best out-of-sample predictive power. More commonly, alternate models are compared based on differences between model-specific AIC_c values (ΔAIC_c). ΔAIC_c values represent the level of empirical support for each model (Burnham and Anderson 2002) where:

ΔAIC_c <2 = strong
2< ΔAIC_c <10 = considerably less
ΔAIC_c > 10 essentially no support

Markov chain Monte Carlo (MCMC) simulation was used to approximate the posterior distribution of parameter values. The posterior distribution was derived by taking every 20th sample from a total of 40,000 simulations. Prior to taking samples from the posterior distributions, 5,000 simulations were conducted to 'burn-in' the jumping distributions. Parameter estimation was done in the 'R' statistical package using the MCMCmetrop1R component of the MCMCPack package.

2.5.2 Wild and Unclipped Stock Model Parameters

We computed the arithmetic mean of marine survival and PSM rates. Standard deviations were computed on log-transformed values standardized around a mean of 0 to be consistent with our simulation approach (eqn. 3). Examination of data revealed that the error structure in marine survival rate and the proportion returning at age 4 was log normal and normal, respectively. The average marine survival rate for Cultus Sockeye was 0.064 with a CV of 0.86 and a lag-1 autocorrelation of 0.34 (n=26). The variance for marine survival rate is likely positively biased due to the very large uncertainty in the estimated number of Cultus recruits in the catch. We therefore examined marine survival rate data for Chilko Sockeye (n=51) where both smolt numbers and catch are relatively well determined. The average marine survival rate for Chilko Sockeye was 0.093 with a CV of 0.63 and a lag-1 autocorrelation of 0.34. For base simulations, we used the average marine survival rate determined from the Cultus data but used the variance term derived from Chilko data as we had no reason to believe the Cultus mean would be biased by high uncertainty in catch estimates. We simulated low and high marine survival rate scenarios using data from 1999-2001 (mean = 0.023) and data from 1952-1990 (mean = 0.072) using the same relative variance for all cases.

Reliable estimates of prespawn mortality for Cultus Sockeye were available for 1945, 1946, 1983, 1991, 1993-1996, 1998, 2002, and 2003. Average PSM for the entire record and 1995-2003 was 0.18 and 0.33 respectively. A frequency distribution of all available data revealed that inter-annual variation in PSM is reasonably approximated by a lognormal distribution. PSM in 1999 and 2000 was likely very high based on the ratio of natural smolt production to parents counted at the Sweltzer Ck. weir. To provide a more complete record to compute PSM statistics that included more recent years, we backcalculated PSM for brood years 1999-2001. We first backcalculated the number of effective spawners for these brood yrs. based on the number of smolts enumerated at the Sweltzer Ck. weir (two yrs. later) and the most likely parameters from the spawner-to-smolt relationship (based on the depensatory Ricker model using prior information on carrying capacity). We then computed PSM based on the ratio of the backcalculated number of effective spawners and the total number enumerated at the weir. Backcalculated PSM values for 1999, and 2000 were 0.86 and 0.63, respectively (compared to backcalculated estimates of 0.86 and 0.88 by M. Bradford, unpublished data). The PSM estimate for 2001 was negative indicating that the backcalculated estimate of the number effective spawners exceeded the observed escapement. We assumed there was no pre-spawn mortality in this year. PSM was measured in 2002 and 2003 (0.12 and 0.23, respectively). We were not able to backcalculate PSM for 2004 and 2005 because smolt data is either not yet available or collected, respectively. Note that years where backcalculation of PSM was done were not included in the stock-recruitment dataset used in the backcalculation or in determining posterior distributions for the population viability modeling.

Using a combination of backcalculated and measured estimates of prespawn mortality, we developed the following 3 prespawn mortality scenarios:

1. **Good**. Average PSM = 0.18 based on all measured estimates of PSM which includes low rates measured in 1946, 1983, 1991, and 1993-4.
2. **Average**. Average PSM =0.33 using all measured estimates from 1995-2003.
3. **Poor**. Average PSM = 0.39 using all estimates from 1995-2003 including 1999-2001 backfilled values.

We tested our simulation approach to ensure that multiplication of the arithmetic marine survival and prespawn mortality rate means by bias-corrected lognormal error terms produced the correct arithmetic mean and lognormal variance values used to drive the simulations. Forecast error was estimated from the posterior distribution of Cultus Sockeye pre-fishery recruits

generated from the smolt-jack forecast model (A. Cass, DFO, Pacific Biological Station). A summary of model parameters used in the simulations is provided in Table 4.

2.5.3 Hatchery Parameters

A Captive Broodstock (CB) program was initiated for Cultus sockeye in 2000 and the plan when this model was developed was to stop collecting spawners from the Sweltzer fence after 2007. Eggs will be taken from hatchery-reared CB spawners until 2012 (e.g. age-5 brood adults) and releases of fry and/or smolts will end in 2014. In this analysis, parameters controlling hatchery production were estimated from release records and estimates of release-to-emigration survival rates (Table 5). The captive broodstock program objective is to capture 50% of the adult spawners at the Sweltzer fence up to 250 wild adult spawners each year, although targets have not been met in some years. Gametes from wild adult spawners taken for brood stock are used in up to 500 different matings to maximize genetic diversity. Approximately 1500 fertilized eggs are then transferred to the Rosewall Creek hatchery for rearing in the CB program. The objective of the CB program is to rear 1500 eggs entirely in the hatchery to produce 500 CB adults. Surplus eggs from the wild spawners taken for brood stock are reared in the hatchery and released as fry or smolts 1 or 2 years after brood collection, respectively. The current capacity of hatchery facilities allows for a total production of 50,000 smolts and 450,000 fed fry per year.

2.5.4 Scenarios

The main emphasis of our analysis was on the effects of harvest rate, hatchery supplementation, and habitat enhancement. Harvest scenarios included fixed exploitation rates ranging from 0-40% in 10% increments, and escapement floor polices with variable exploitation rates above the floor (Table 6, Fig. 3). We explored the effects of marine and pre-spawn mortality rates and alternate assumptions about the relative survival of hatchery-origin (clipped smolts) and the relative reproductive performance of clipped fish spawning in the wild. We explored the effects of freshwater habitat enhancement on naturally- and hatchery-produced juveniles (effective 2008-2015 or 2008-2035). Note that the habitat enhancement adjustments to the spawner-to-smolt relationship and to hatchery production only affect those cohorts when their entire freshwater lifecycle occurs during the period when enhancement is implemented. We also explored the effects of increasing hatchery capacity where captive broodstock or supplementation (e.g. fry and smolt releases in brood year +2) programs were operated from 2007 through 2015 (broodstock collection ends in 2015). Finally, we explored combinations of recovery options that included hatchery supplementation and habitat enhancement. A total of 2,000 simulation trials were run for each of the 128 scenarios to minimize (<1%) the Monte Carlo variation in the cumulative mean across trials. Results were summarized by plotting the average value across trials for each scenario as well as the 20^{th} and 80^{th} percentiles as error bars.

3.0 RESULTS

Both Ricker and depensatory models fit the data well (Fig. 4). Most likely parameters for the Ricker model fit to the data which excluded years with predator or unknown hatchery additions or pre-spawn mortality rates were =4.11 (stock productivity = 61 smolts/spawner), =.04 (effective spawners that produces maximum smolt numbers = 250,000), and =0.64. The Ricker model had a lower AIC_c score compared to the depensatory model based on the full dataset and an equivalent AIC_c score based on the smaller dataset (Table 7). As the differences between AIC_c scores were <2, we conclude that there is relatively strong support for both models (Burnham and Anderson 2002), especially in the case of the smaller dataset. The probability that the improved fit associated with the depensatory model was due to chance alone was 0.46 for the full dataset. In other words, the depensatory term did not significantly improve model fit. However, the depensatory term was marginally significant (p=0.097) when applied to the smaller dataset.

The extent of depensatory mortality could be increased by assuming more prior information on the strength of depensation, and to a lesser extent, prior information on density dependence (Fig. 4). Quantile-quantile plots were used to compare the distribution of residuals from the best-fit models to the expected distribution if the residuals (in log space) are normally distributed (eqn. 14, Fig. 5). Departures from normality indicate that the model structure is inconsistent with the data, either in the assumed form of the model or the error structure. Residuals were reasonably normally distributed in all cases. Plots of the residuals as a function of the number of effective spawners showed that the Ricker model tended to overpredict smolt numbers at low stock size (-'ve residuals), while the depensatory model eliminated this minor but potentially important bias (Fig. 6). There were no trends in residuals over time for stock-recruitment models fit to the subset of data, suggesting that freshwater productivity has been relatively stationary through time (Fig. 7.

Subsequent analyses will be based exclusively (with one exception) on the depensatory model fit to the smaller dataset where non-representative years were excluded (n=30 dataset). We chose the depensatory model and smaller dataset because:

1. The residuals from the depensatory model provided better estimates of smolt production at low stock size (Fig. 6) and had slightly better out of sample predictive power (Table 7).
2. Years with predator removal or unknown hatchery contributions or pre-spawn mortality should not be considered as part of the natural baseline for the production relationship for the Cultus stock.
3. Including depensatory recruitment provides a more conservative simulation of stock rebuilding which is consistent with a precautionary management approach.

Posterior distributions showed considerable confounding between α, β, and δ estimates. As seen in many stock-recruitment datasets, there was a positive relationship between α and β (Fig.'s 8 and 9). The data indicate either a more productive stock with a lower carrying capacity (larger β as capacity = $1/\beta$), or a less productive one with a higher capacity. There was considerable confounding between depensation and productivity which in part reduced the confounding between α and β. In order to explain the data, higher estimates of depensation (larger values of δ) must be offset by higher estimates of productivity (larger values of α). We were not able to get the posterior distribution to converge when applying the depensatory model assuming uniform priors (Fig. 8). There is simply not enough information in the data to estimate both α and . The model that used moderate information on carrying capacity (Fig. 9) from the Shortreed et al. model (2001) did converge. As there is little information about carrying capacity in the data, the posterior distribution for was largely determined by the prior (Fig. 10).

When assuming no prior information about density dependence, many of the stock-recruitment curves from the posterior distribution showed evidence of depensation. In order to fit observed smolt production at low stock sizes, the model estimated strong density dependence, which is not apparent in the data (Fig. 11, top). The model that assumed moderate prior information on density dependence eliminated stock-recruitment curves with very strong density dependence at the cost of reducing the extent of depensation (Fig. 11, bottom). We used the depensatory Ricker model with prior information on density dependence for population viability simulations because the prediction of carrying capacity in the absence of using this prior information was unrealistically high given the findings of Shortreed et al. (2001). While excluding the prior from Shortreed et al. (2001) would lead to more conservative predictions concerning stock recovery, there is no rational for excluding the substantive information on the carrying capacity of Sockeye lakes. The most likely parameters for the selected model were: α=4.54 (maximum productivity without depensation = 93 smolts/spawner); =0.12 (83,000 effective spawners required to attain maximum smolt production); =0.62; and =0.30 (productivity reduced by ½ at 3,000 effective spawners.), respectively.

A critical structural assumption of the model regarding the effects of improved freshwater enhancement on smolt production is that the enhancement effect occurs after density dependence. This assumption leads to the following relationship that describes the relative increase in freshwater productivity required to offset an increase in harvest rate,

$$E = 1 + \frac{h_2 - h_1}{1 - h_2} \tag{23}$$

where, E is the relative increase in the number of smolts produced at any spawner density (eqn. 1), h_1 is the base harvest rate (e.g. 0.1), and h_2 is the higher harvest rate being considered (Fig. 12). A doubling in the number of smolts produced per spawner is required to offset a harvest rate of 0.5 relative to no harvest. However, the relationship is not linear and implies that more modest increases in freshwater productivity are required to offset lower harvest rates (e.g. a 1.2-fold increase in productivity is required to offset a harvest rate of 0.2 relative to no harvest).

The hatchery component of the model was run independently to examine how the relationship between the number of broodstock collected and the number of effective hatchery-origin smolts passing the Sweltzer Ck. fence changed as a function of hatchery parameters. Predictions include mortality in the lake from release to arrival at the fence and are calculated for both captive broodstock and supplementation operations. Under default parameters, the extreme productivity of a captive broodstock program is apparent (Fig. 13). This is the ultimate stock-recruitment curve with smolt production approaching capacity even if only 1 pair of fish is obtained for broodstock. Stock productivity is almost infinite because only 1500 eggs from the original broodstock are required to generate 500 captive adults that will provide sufficient eggs to meet the fry and smolt rearing capacities in the hatchery for the next generation. As broodstock numbers increase, the number of effective smolts slowly rises at a rate determined by the ratio of fed fry and smolt hatchery capacities, and the survival rates of unfed and fed fry in the lake. The productivity of a supplementation program, while lower than for the captive broodstock program, is about 850 effective smolts/spawner (ca. 25,000 smolts produced from 30 spawners). This productivity is 10-fold higher than the estimate from the historical dataset in the absence of depensatory effects (from Fig. 4). The slope of the hatchery recruitment curve beyond the inflection point of the supplementation curve, and the slope of the captive program curve, increases with higher in-lake survival rates of fed fry (Fig. 13b). However, there is not a 1:1 relationship between increases in in-lake survival and smolt production. This occurs because most of the smolt production comes from smolts released at the fence. In-lake survival rates of unfed and fed fry are very low, so these fish do not contribute substantively to smolt production. Increasing smolt capacity does not change the slope of recruitment curves, but it does increase the overall magnitude of recruitment rate and the number of broodstock required to reach the inflection point of the supplementation program relationship (Fig. 13c). Decreasing survival rate of smolts released into the lake to the Sweltzer Ck. fence results in a downward shift in hatchery stock-recruitment relationships (Fig. 13d).

Two realizations of the model under the moderate survival-PSM scenario (Table 6) and the default hatchery survival assumptions (Table 5) with termination of the current captive broodstock program in 2007 and the 1.5k harvest policy (Table 6) show the considerable variation in outcomes among Monte Carlo trials (Fig. 14). The realization that shows a declining trend (Fig. 14, bottom) has probabilities of attaining recovery objectives I and II for all unclipped fish of 19% and 7%, respectively compared to the realization where the population has stabilized where the probabilities are 44% and 9%, respectively. The averaged realized harvest rates for the declining and sustainable realizations are 14% (inter annual CV=177%) and 31% (CV=90%), respectively.

Recovery performance was very sensitive to the assumed marine and pre-spawn survival rates (Fig. 15). Under the average survival rate scenario (Table 6) the abundance-based recovery objective is attained at a probability of about 70% when there is no harvest and at a

probability of less than 30% at a fixed harvest rate of 40%. The probability is less than 10% under the most aggressive harvest policy (escapement floor of only 500 spawners). Under the latter harvest scenario there is virtually no chance of an increase in the average abundance at the end of the simulation (2034-2037). The probability of extinction rises from less than 10% under no harvest, to over 80% under the most aggressive harvest regime. When survival is high there is less variation in conservation-based performance measures across harvest rates and there are large gains in average long-term (2006-2037) realized harvest rate on Late run Fraser sockeye. At high survival there was virtually no risk of extinction except under the two most aggressive harvest policies. When survival is very low the model predicts that the Cultus population is not sustainable, regardless of the harvest rate.

Doubling the capacity of the hatchery to produce smolts and extending the operation through 2015 as a captive broodstock or supplementation program had little effect on most recovery statistics with the exception of extinction probabilities (Fig. 16). The extended programs reduced extinction probabilities by at least 50% of the baseline values under most harvest regimes. In the last 4 yrs. of broodstock collection of the extended operations, at least ½ of the effective spawners in Cultus Lake would have been born in the hatchery. Recovery statistics were marginally improved by increasing hatchery capacity (Fig. 17). Interestingly, there is little change in the percentage of unclipped fish that spawn naturally when hatchery capacity is increased. Larger numbers of unclipped fish (naturally-produced progeny of clipped parents) offset the effect of increased numbers of clipped fish spawning in the lake. However, the ratio of wild fish, as defined by the DFO wild salmon policy, to total spawners would decline under the extended hatchery programs and with increasing hatchery smolt production. Recovery statistics were sensitive to assumed survival rates of hatchery fish after release and their relative reproductive success compared to wild fish (Fig. 18). Under the most pessimistic scenario we examined (ϕ_H=0.2, ϕ_U=0.5) the reduction in extinction probability associated with increasing hatchery capacity and extending a supplementation program through 2015 are considerably reduced compared to the default scenario (ϕ_H=0.5, ϕ_U=1).

The benefits of freshwater habitat enhancement depended on both the magnitude and duration of treatment (Fig. 19). Substantive improvements to overall productivity (E=1.5) or reductions in the extent of depensation (E_d=0.5) provided little improvement in recovery objectives when the treatment duration was short (2008-2015). Extending the duration of treatments for the entire 8 generations of the simulation resulted in minor improvements to objectives I and II and reduced extinction probabilities substantially, especially at more aggressive harvest rates.

Model performance was very sensitive to the form of the stock-recruitment spawner-to-smolt relationship (Fig. 20). When we assumed no depensation by using the posterior distribution for the standard Ricker model (Fig. 4), abundance- and growth-based performance measures increased 2 to 3-fold under the more aggressive harvest regimes relative to simulations based on the depensatory model. There was little difference in the final population sizes between the two stock-recruitment scenarios, but the population recovered more quickly in the absence of depensation resulting in better recovery performance. This dynamic is reflected in the higher realized harvest rate and the elimination of extinction risk in the absence of depensation.

Finally, we simulated an aggressive recovery strategy where both habitat enhancement and continuation of a supplementation hatchery program were combined (Fig. 20). We assumed that habitat enhancement occurred for the duration of the simulation and resulted in an increase in freshwater productivity and in-lake survival of hatchery fish of 50% (E=1.5, $E_{H,UFF}$ and $E_{H,FF}$ = 1.5), and a similar decrease in depensation (E_d=0.5). We simulated a hatchery supplementation program with a smolt capacity of 100,000 extending through 2015. This recovery strategy resulted in large improvements in all performance measures.

4.0 CONCLUSIONS

As for any population viability analysis, the results presented here should be viewed with healthy skepticism. The modeling exercise was useful for examining the relative benefits of alternate recovery options and for highlighting priorities for data collection and research. The absolute probabilities predicted by the model were very sensitive to the assumed survival regimes that cannot be forecasted. Under the optimist marine survival-PSM scenario there is no need to continue hatchery supplementation and the most aggressive harvest regime we examined still allowed the Cultus Sockeye population to recover. Under the worst-case survival-PSM scenario, the long-term viability of the Cultus population is very low unless the current captive broodstock program is extended.

Two of three possible harvest strategies were evaluated in this analysis. We simulated fixed harvest rate strategies from 0-40% as well as escapement-floor policies based on the pre-fishery recruitment forecast for the Cultus Lake population. We did not perform any simulations based on harvest rates determined from the FRSSI model, which are used to optimize yield and recovery for the Late run aggregate. While the analysis we conducted was a useful exercise to explore the potential benefits of a Cultus sockeye floor policy relative to a fixed exploitation rate strategy, implementation of such a policy is unlikely. However, results from the fixed exploitation simulations should be of use in future planning activities. It should be noted that the harvest simulations that were completed for this report included the effects of error associated with the pre-season forecasts for the Cultus population only. They did not include the effects of other aspects of management error (i.e., ability to attain target catch or exploitation rate) or potential biases (tendency to over-shoot harvest targets of small populations). Future runs of the Cultus model should consider all components of forecasting and harvest implementation error and biases.

We have assumed no interaction between juvenile fish released from the hatchery and wild juveniles in Cultus Lake. Hatchery benefits could be greater if increased numbers of juvenile fish reduce depensatory effects, or less if density dependent competitive interactions reduce the production of both wild and hatchery fish. This aspect of the model requires further refinement but there is little data currently available to address this issue. Ideally, a research program focused on enhancement of Cultus Lake sockeye should examine competitive interactions between wild and hatchery fish, as well as predator-prey interactions between pikeminnow and all juvenile sockeye. In addition, the authors were recently made aware that the freshwater survival of hatchery fry releases may have improved due to improved release techniques (e.g. mid lake releases by vessel). As a result, survival rate parameters (and other fixed parameters) should be reviewed and re-estimated as necessary in conjunction with any new analyses done in the future.

Finally, our model does not simulate changes in the genome of wild fish resulting from a long-term hatchery operation. This simplifying assumption is perhaps reasonable when simulating the default hatchery scenario where captive broodstock collection ends in 2007. This end date was designed to eliminate the probability of using fish with hatchery origins as broodstock. However, simulations of continued hatchery operation, especially when the number of broodstock taken is low due to weak returns, would likely result in significant reduction in effective population size. This in turn could likely lead to significant losses in reproductive success as well as loss of evolutionary potential (Berejikian and Ford, 2004).

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TABLE 1.
Summary of model indices and state variables. Note list of error terms is not inclusive of all stochastic elements in the model but only those defined in text describing model.

Variable or subscript	Description
Indices	
Stock type (st)	St= W for wild, H for hatchery, U for unclipped
Year (t)	
State Variables	
Sm	# of Smolts
p	Proportion of effective spawners (pW+pH+pU=1)
Sp	# of spawners
R	# of pre-fishery recruits
pa	Proportion of adults returning by age
MS	Marine survival rate
Esc	# of spawners at weir
C	# of pre-fishery recruits that are caught
$\hat{R}$	# of forecasted pre-fishery recruits
Brood	# of spawners taken for broodstock
h	Harvest rate (a state variable if not fixed)
PSM	Pre-spawn mortality rate
State Variables for Hatchery Stock	
TEggs	Total eggs collected for hatchery production at fence
SupEggs	# eggs used to produce fry to be released into lake
CBEggs	# eggs produced from captive broodstock
UFF	# unfed fry produced in the hatchery
FF	# fed fry produced in the hatchery
UFlake	# unfed fry released into lake
FFlake	# fed fry released into lake
UFFsmolt	# of unfed fry required to meet hatchery smolt capacity
SMlake	# of smolts released into lake
Error Terms (used in text)	
	Residual from spawner-smolt relationship
	Residual from expected marine survival rate
	Residual from expected recruitment

TABLE 2.
Performance measures used to assess population trajectories of the effective number of spawning Sockeye in Cultus Lake and the allowable harvest rate on late-run Fraser River Sockeye. N_t refers to the number of effective wild or wild + unclipped spawners in year *t*. Avg. denotes an average across return years.

Recovery Objective	Rule	Statistic
Ia – Generational abundance	$Avg(N_t:N_{t-3}) >= GenLimit$	% yrs objective met
Ib – Cycle abundance	$N_t > CycleLimit$	% yrs objective met
I – Recovery objective 1	Ia AND Ib	% yrs objective met
II – Population growth	Generational growth ($Avg(N_t:N_{t-3})>Avg(N_{t-4}:N_{t-7})$) AND cycle over cycle growth in 3 of 4 consecutive yrs (e.g. $N_t>N_{t-4}$, AND $N_{t-1}>N_{t-5}$,...).	% yrs objective met
Final population growth	$R = \frac{Avg(N_{2034}:N_{2037})}{Avg(N_{2006}:N_{2009})}$	Ratio of average abundances
Extinction	$N_{T-1} < ExtLimit$	True/False per simulation (or % of simulations over multiple trials)
Harvest	Average realized harvest rate over simulation	Average and CV
Proportion of hatchery-origin spawners	Ratio of clipped spawners to total spawners	Average in last 4 yrs of broodstock collection and last 4 yrs of simulation

TABLE 3.
Initial Conditions used for simulation.

Calender Year	Wild Spawners	Hatchery Spawners	Wild Smolts	CB Eggs	Wild Eggs	Unfed Fry	Hatchery Smolts
1999	1,668	0					
2000	152	0					
2001	255	0					
2002	4,235	0					
2003	1,485	0	9,782				2,183
2004	43	15	109,843				7,178
2005	112	3	82,096	1,141,008	188,500	659,387	19,447

TABLE 4.
Summary of default parameters used in simulation. Note that α, β, [illegible], and δ values used in the simulation are random draws from a posterior distribution generated from the historic spawner and smolt data and prior distributions specified in the table. Other parameter values used in alternate model scenarios are shown in Table 6. See Table 5 for parameters that influence hatchery production.

Parameter	Description	Estimate
Stochastic Variables		
α	Smots/spawner at low stock size	Posterior (uniform prior)
β	Density dependence in smolt production	Posterior(normal prior: $1/\mu_{\beta}$=83,000, σ_{β}(CV)=0.25)
δ	Depensation in smolt pr[illegible]duction	Posterior (uniform prior)
	SD of spawner-to-smolt relationship	Sample from posterior
μ_a	Mean proportion at age a = 4	4.695 (in logit) 0.96 (in linear)
σ_a	Standard deviation in proportion at age a=4	2.229 (in logit) 0.07 (in linear)
μ_{ms}	Arithmetic mean marine survival rate	0.064 (see Table 6)
σ_{ms}	SD of log-transformed marine survival rate	0.63 (see Table 6)
ρ_{ms}	Lag-1 autocorrelation in marine survival rate	0.34 (see Table 6)
μ_{psm}	Arithmetic mean of pre-spawn mortality rate	0.33 (see Table 6)
σ_{psm}	SD of log-transformed pre-spawn mortality rate	0.6 (see Table 6)
ρ_{psm}	Lag-1 autocorrelation in pre-spawn mortality rate	0
σ_{for}	SD of pre-season forecast (log space)	1.0
Deterministic Variables		
E	Relative increase in number of naturally-spawned smolts produced due to freshwater enhancement	See Table 6
E_d	Relative decrease in extent of depensation on naturally-spawned smolts due to freshwater enhanement (e.g. predator removal)	See Table 6
h_h	Harvest rate due to fishing	See Table 6
GenLimit	Generational average population size that must be equal to or exceeded to meet recovery objective 1a	1000
CycleLimit	Cycle-specific population size that must be equal to or exceeded to meet recovery objective 1b	500
ExtLimit	Population size that must be equal to or exceeded to avoid quasi-extinction	100

TABLE 5.
Summary of model parameters that determine hatchery production. Other parameter values used in alternate model scenarios are shown in Table 6.

Parameter	Description	Estimate
h_H	Maximum harvest rate on unclipped returns to weir due to broodstock capture	0.5
MaxTake	Maximum number of unclipped returns taken for broodstock	250
F	Average fecundity of fish taken for broodstock	3,750
sx	Proportion of females in broodstock	0.5
CBEggTake	Number of eggs required to attain adult captive broodstock capacity in hatchery	1,500
EggsFromCB	Total number of eggs produced from captive brood maturing at 'iage'	iage=3: 150,000 iage=4: 250,000 iage=5: 68,750
FryCap	Capacity of hatchery to produce fed fry for release	450,000
SmoltCap	Capacity of hatchery to produce smolts	50,000 (see Table 6)
EUFsurv	Egg to unfed fry survival rate for eggs taken from broodstock	0.9
CB_EUFsurv	Egg to unfed fry survival rate for eggs taken from captive broodstock	0.47
UFFFFsurv	Unfed fry to fed fry survival rate in the hatchery	0.94
FFSMsurv	Fed fry to smolt survival rate in the hatchery	1.0
LkUFSMsurv	Survival rate from release of unfed fry in lake to migration past fence as smolt	0.015
LkFFSMsurv	Survival rate from release of fed fry in lake to migration past fence as smolt	0.03
LkSMsurv	Survival rate from release of smolts in lake to migration past fence	Released in lake: 0.12 Released at fence: 1.0
st	Relative marine survival of hatchery (st=H) and unclipped stocks (st=U)	H =0.2, U =1.0 (see Table 6)
E_H	Relative improvement in in-lake survival of hatchery fish due to habitat improvement	(see Table 6)

TABLE 6.
Summary of management scenarios and parameter values used in analysis. Harvest rate rules will likely produce 2006 exploitation rates shown in the Scenario column. Baseline parameter values are highlighted in bold.

Parameter Name	Parameters	Scenario	Values
Harvest Rate	E_{min}, h, ER_{cap}	Fixed exploitation	0, (0,.1,.2,.3,.4), 1
		0.5k	500, 1, 0.65
		3.5k	3500, 1, 0.65
		10k	10000, 1, 0.65
Marine Survival Rate	μ_{ms}/σ_{ms} $/\rho_{ms}/\omega_{t-1}$	Low [1]	0.023/0.63/0/0
		Moderate [2]	**0.064/0.63/0.34/-.51**
		High [3]	0.072/0.63/0/0
Prespawn Mortality Rate	μ_{PSM}/σ_{PSM} $/\rho_{PSM}$	Low [4]	0.18/0.87/0
		Moderate [5]	**0.33/0.60/0**
		High [6]	0.39/0.75/0
Freshwater Habitat Enhacement	$E/E_d/E_{H,SM}/$	**None**	**1.0**
	$E_{H,FF}/E_{H,UF}$	Short (2008-2015)[7]	1.5/0.5/1.0/1.5/1.5
		Extended (2008-2035)	1.5/0.5/1.0/1.5/1.5
Survival of Hatchery Smolts Relative to Wild Smolts	Φ_H	Low	0.2
		Expected	**0.5**
Reproductive success of clipped spawners	Φ_U	Low	.5
		Expected	**1**
Hatchery Capacity	SmoltCap	**50,000 smolts**	**50,000**
		100,000 smolts	100,000
		150,000 smolts	150,000
Hatchery Operation		**CB ends 2007**	
		Suppl. To 2015	
		CB to 2015	

[1] Low marine survival scenario determined from 1999-2003 brood year survival estimates (only estimates available between 1991 to present).
[2] Moderate marine survival scenario determined from all available survival estimates (1952 to present).
[3] High marine survival scenario determined from 1952-1990 survival estimates.
[4] Low pre-spawn mortality scenario determined from PSM measured estimates from 1945 to 2003 brood years.
[5] Moderate pre-spawn mortality scenario determined from 1995-2003 PSM measured estimates.
[6] High pre-spawn mortality scenario determined from 1995-2003 PSM measured estimates and 1999-2000 back-calculated estimates.

[7] We assume hatchery smolts are released at fence, so there is no effect of habitat enhancement on their survival rate. We assume that the benefit of habitat enhancement on unfed and fed fry is equivalent and results in a 50% increase in the base survival rate.

TABLE 7.
Summary of stock-recruitment model comparison statistics. Statistics are provided for the analysis based on all yrs. of data and a subset of data where yrs. with predator control, and unknown hatchery contributions or pre-spawn mortality rates were excluded. The X2 probability represents the probability that differences in model fit could be due to chance alone. Models with lower AIC_c scores have better out-of-sample predictive power.

		Ricker	**Depensatory**		
# of Parameters		3	4		
	Sample Size	**Log Likelihood**	**Log Likelihood**	**2 * Log Like. Difference**	**X^2 Prob.**
All Yrs.	48	-54.616	-54.345	0.542	0.462
Subset	30	-29.352	-27.976	2.752	0.097
				AIC_c	
AIC_c	48	**115.78**	117.62	1.84	
	30	65.63	**65.55**	0.08	

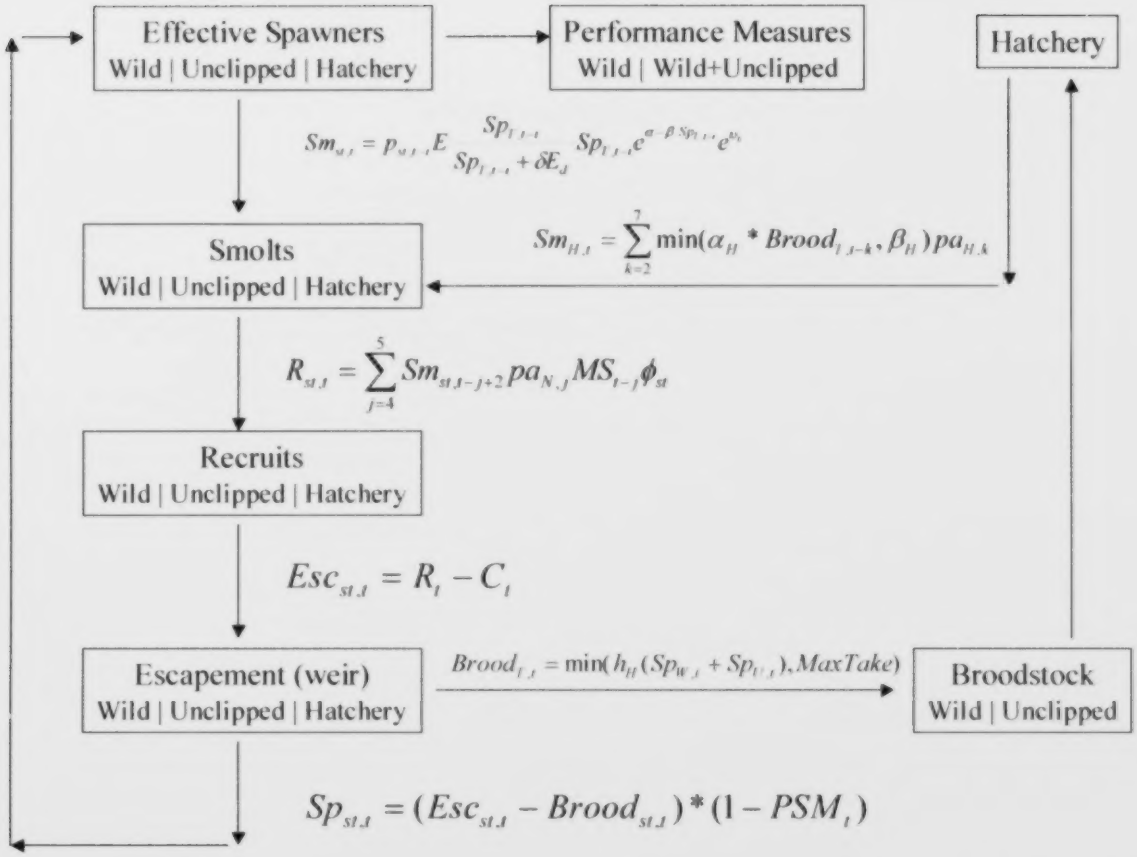
Effective Spawners
Wild | Unclipped | Hatchery
Performance Measures
Wild | Wild+Unclipped
Hatchery
$Sm_{s,t} = p_{s,t-1} E \frac{Sp_{t-1}}{Sp_{t-1} + \delta E_t} Sp_{t-1} e^{\alpha - \beta Sp_{t-1}} e^{\varepsilon_t}$
$Sm_{H,t} = \sum_{k=2}^{7} \min(\alpha_H * Brood_{t-k}, \beta_H) pa_{H,k}$
Smolts
Wild | Unclipped | Hatchery
$R_{st,t} = \sum_{j=4}^{5} Sm_{st,t-j+2} pa_{N,j} MS_{t-j} \phi_{st}$
Recruits
Wild | Unclipped | Hatchery
$Esc_{st,t} = R_t - C_t$
Escapement (weir)
Wild | Unclipped | Hatchery
$Brood_{t,t} = \min(h_H (Sp_{W,t} + Sp_{U,t}), MaxTake)$
Broodstock
Wild | Unclipped
$Sp_{st,t} = (Esc_{st,t} - Brood_{st,t}) * (1 - PSM_t)$

FIGURE 1.
Overview of Cultus Lake Sockeye population viability model. See text for description of equations and additional ones not shown here.

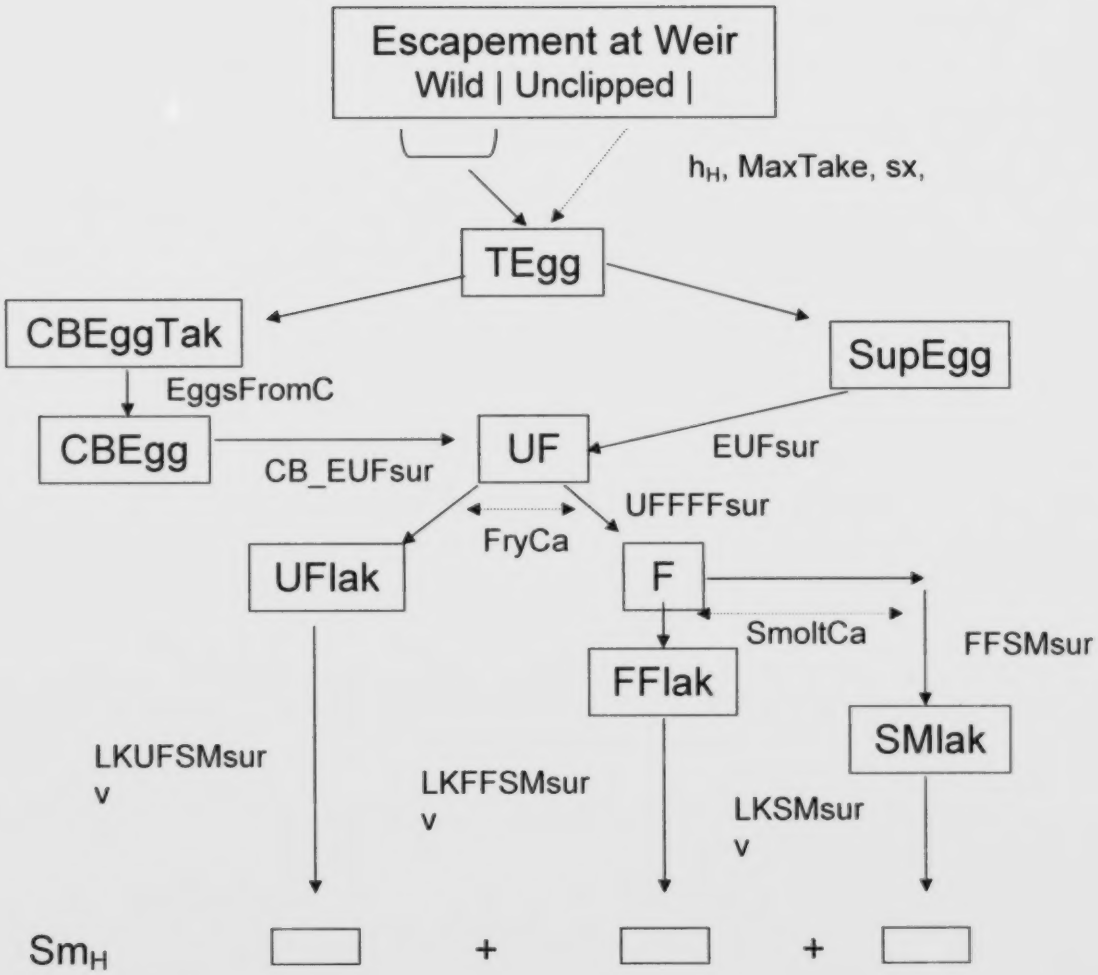

FIGURE 2.
Overview of hatchery component of Cultus Lake Sockeye population viability model. See text and Tables 1 and 5 for definition of variable names.

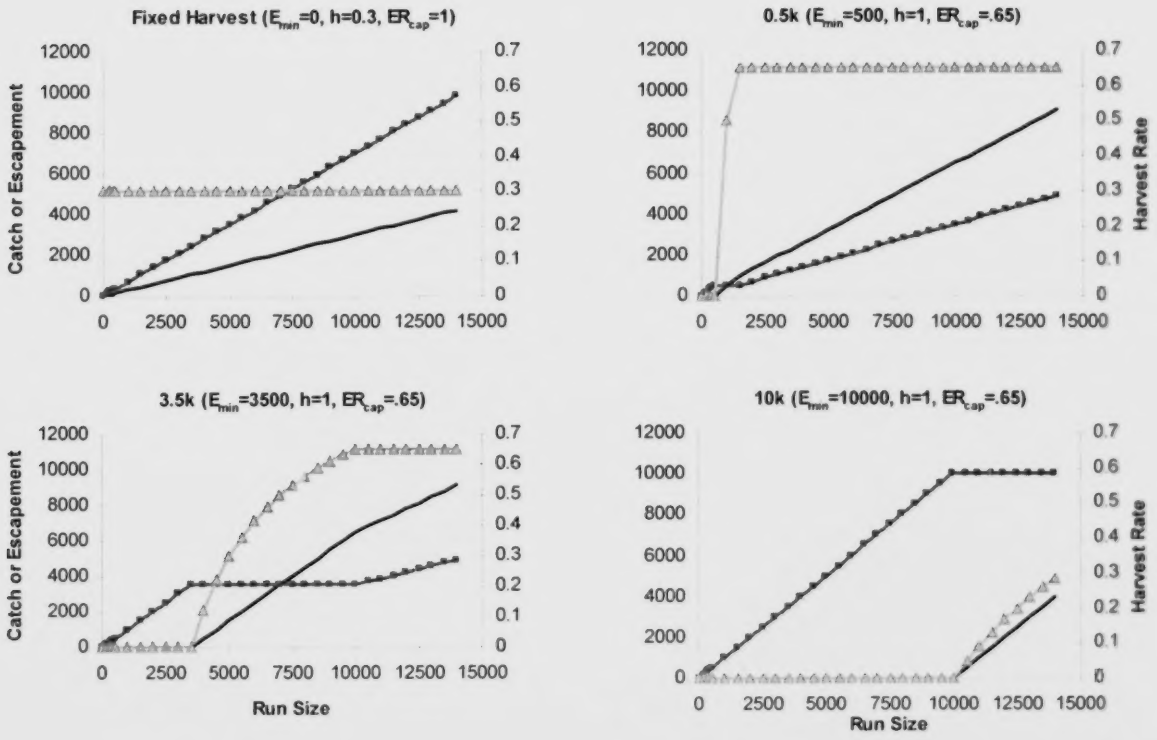

FIGURE 3.
Realized catch, escapement, and harvest rate under a range of pre-fishery recruitments (run size) assuming no forecast or management implementation error. Catch, escapement, and harvest rate are denoted by solid lines, lines with squares, and lines with triangles, respectively. Graphs are based on a fixed exploitation rate of 0.3 (lop-left) and a range of escapement floor policies (E_{min}=500, 3500, and 10000 spawners).

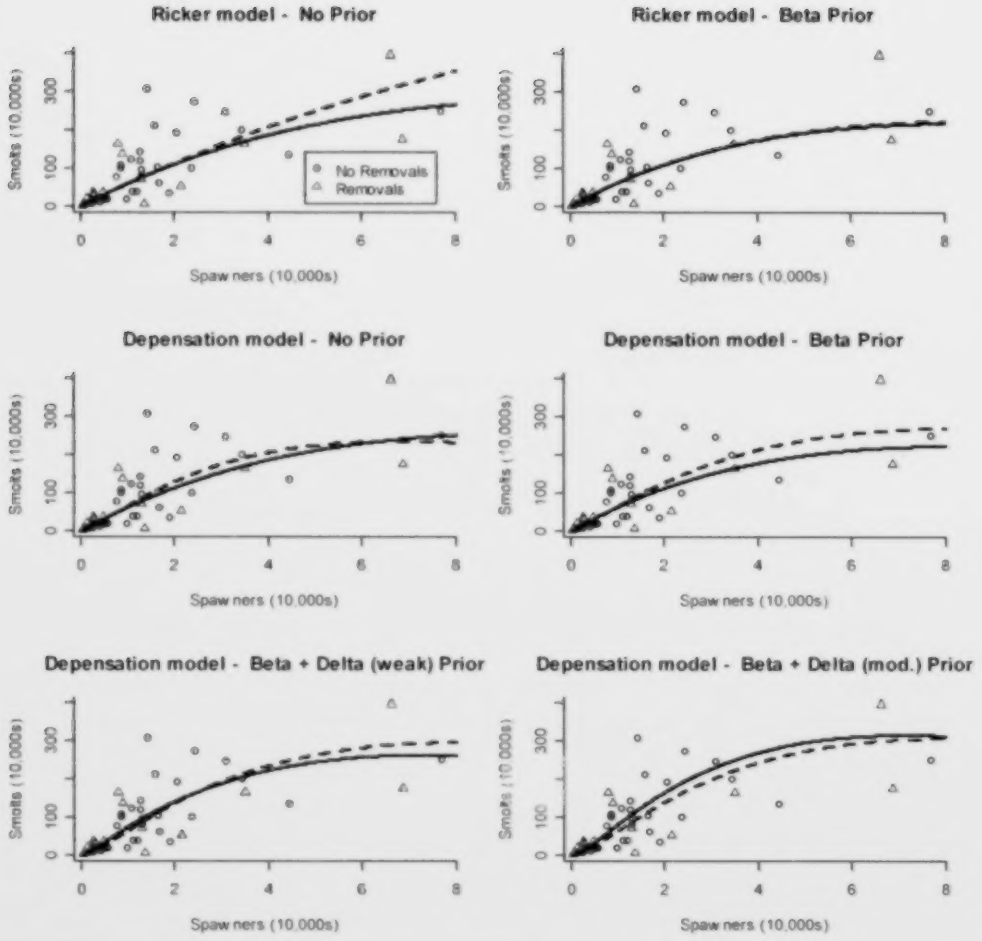
Ricker model - No Prior
Ricker model - Beta Prior
Depensation model - No Prior
Depensation model - Beta Prior
Depensation model - Beta + Delta (weak) Prior
Depensation model - Beta + Delta (mod.) Prior
Smolts (10,000s)
Spawners (10,000s)
No Removals
Removals

FIGURE 4.
Most likely Ricker (δ fixed at 0) and depensatory-Ricker model fits to the data assuming no prior information on parameter values, moderate prior information on the density dependent parameter (μ_β =1/ 8.3, σ_β=0.25), and with weak (μ_δ=0.7, σ_δ=0.5) and moderate (μ_δ=0.7, σ_δ=0.25) prior information on the depensation parameter. Solid lines represent best-fit models using all the data (n=48, open circles), while dashed lines are models fit to a subset of data (n=30) where years with predator removals, and unknown hatchery inputs and pre-spawn mortality rates were excluded (yrs. excluded from subset denoted by open triangles).

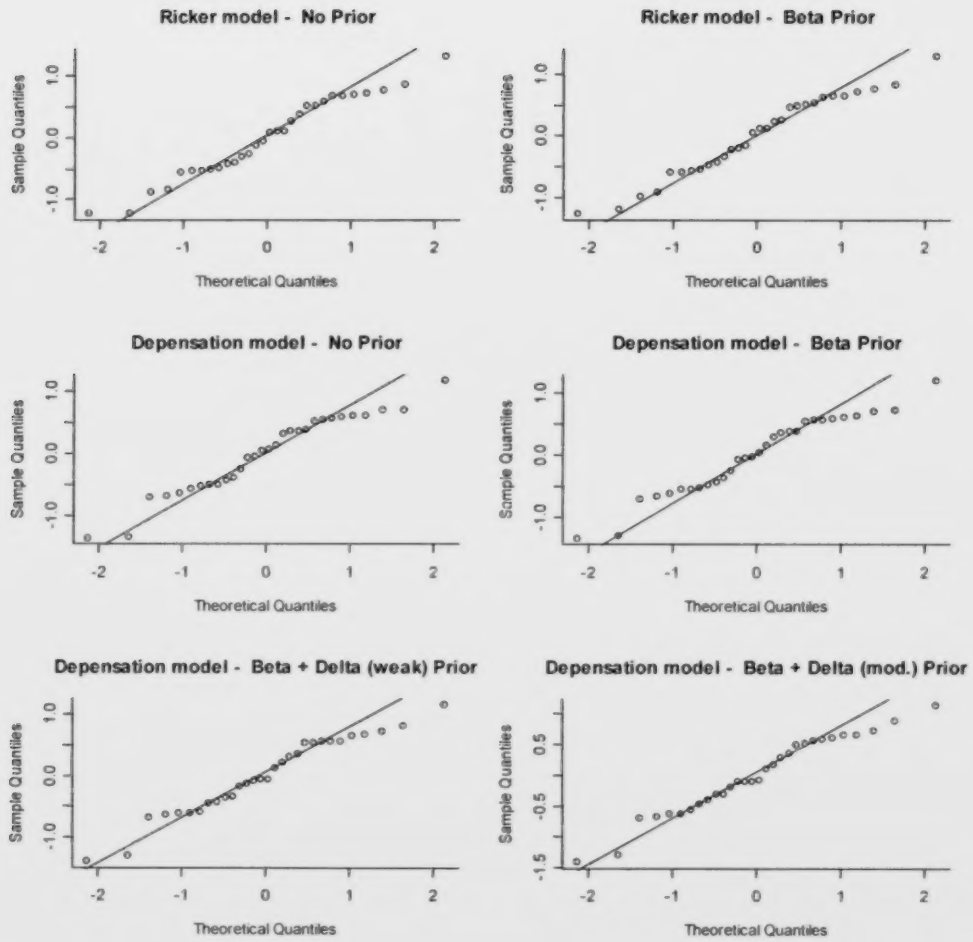
Ricker model - No Prior
Ricker model - Beta Prior
Depensation model - No Prior
Depensation model - Beta Prior
Depensation model - Beta + Delta (weak) Prior
Depensation model - Beta + Delta (mod.) Prior
Sample Quantiles
Theoretical Quantiles

FIGURE 5.
Quantile-quantile plots of most likely Ricker (δ fixed at 0) and depensatory-Ricker model fits to a subset of data (circles in Figure 4) assuming no prior information on parameter values, moderate prior information on the density dependent parameter (μ_β =1/ 8.3, σ_β=0.25), and with weak (μ_δ=0.7, σ_δ=0.5) and moderate (μ_δ=0.7, σ_δ=0.25) prior information on the depensation parameter. The greater the deviance from the 1:1 line, the less the residuals from the model follow a normal distribution.

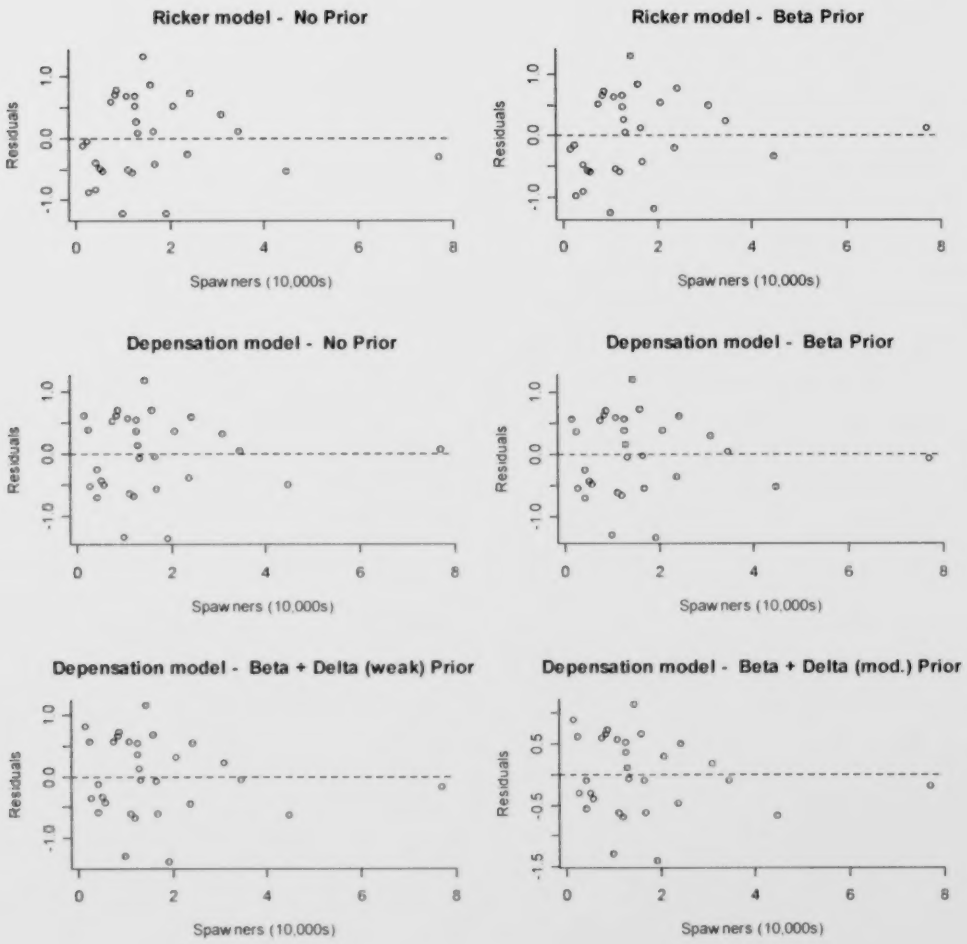
Ricker model - No Prior
Ricker model - Beta Prior
Depensation model - No Prior
Depensation model - Beta Prior
Depensation model - Beta + Delta (weak) Prior
Depensation model - Beta + Delta (mod.) Prior
Residuals
Spawners (10,000s)

FIGURE 6.
Residuals of stock-recruitment fits as a function of number of spawners. Residuals are based on most likely Ricker (δ fixed at 0) and depensatory-Ricker models fit to a subset of data (circles in Figure 4) assuming no prior information on parameter values, moderate prior information on the density dependent parameter (μ_β =1/ 8.3, σ_β=0.25), and with weak (μ_δ=0.7, σ_δ=0.5) and moderate (μ_δ=0.7, σ_δ=0.25) prior information on the depensation parameter.

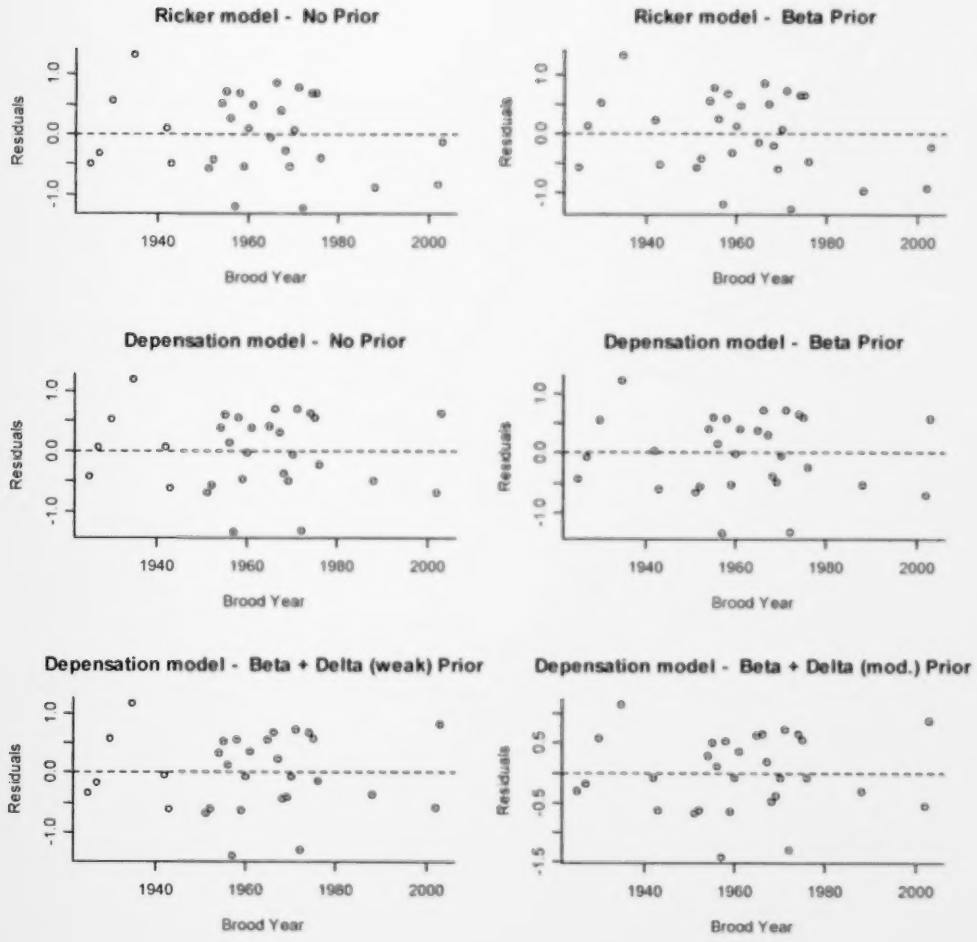

FIGURE 7.
Residuals of stock-recruitment fits as a function of brood year. See Figure 6 for caption details.

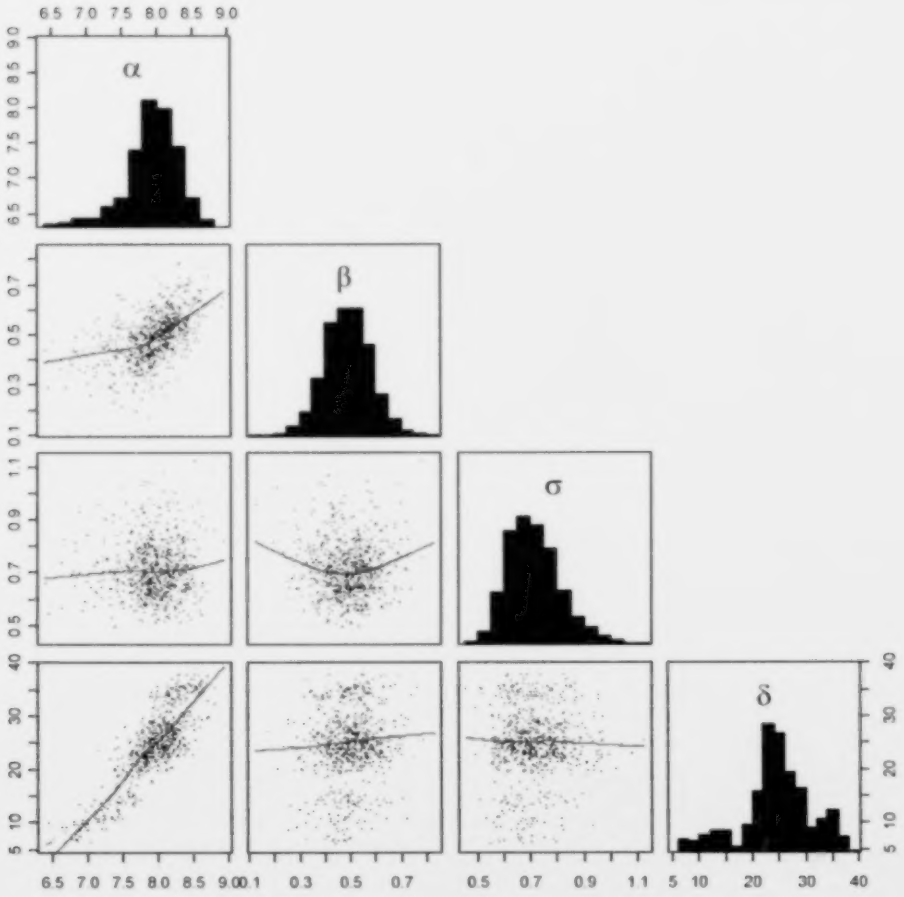

FIGURE 8
Posterior distributions (histograms) and pair plots from an MCMC sample computed using the depensatory Ricker model and the data subset (n=30) assuming no prior information on density dependent or depensatory parameters

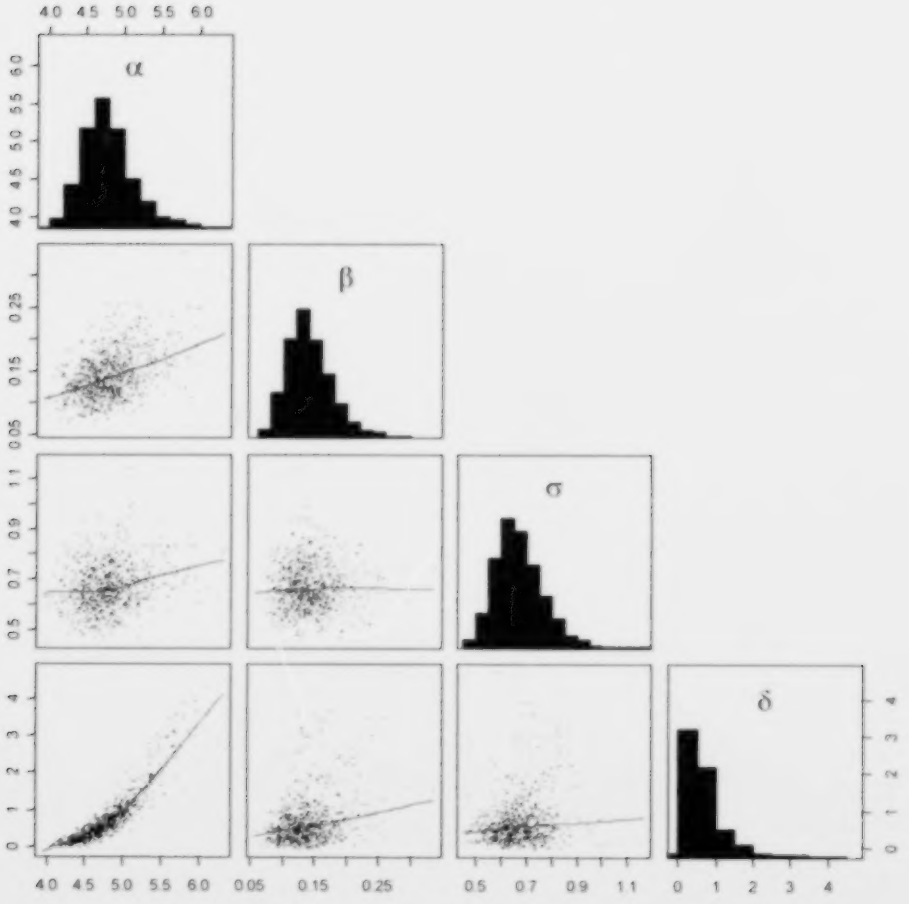

FIGURE 9.
Posterior distributions (histograms) and pair plots from an MCMC sample computed using the depensatory Ricker model and the data subset (n=30) assuming moderate information in the density dependent term (μ_β=0.7, σ_β=0.25).

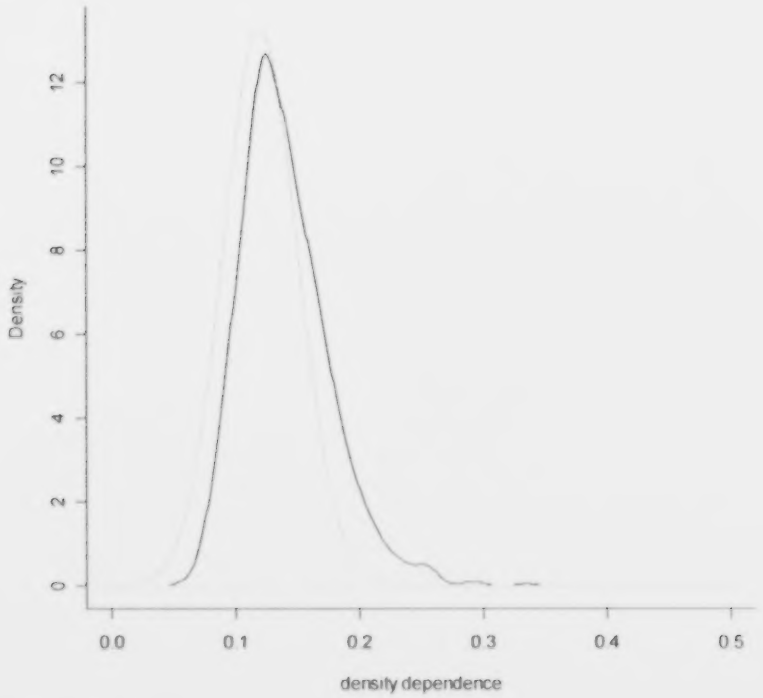

FIGURE 10.
Comparison of the posterior distribution (solid line) for the density dependent term ( ) of the depensatory Ricker model assuming moderate prior information (μ_{β}=0.7, σ_{β}=0.25) and the prior distribution (dashed line).

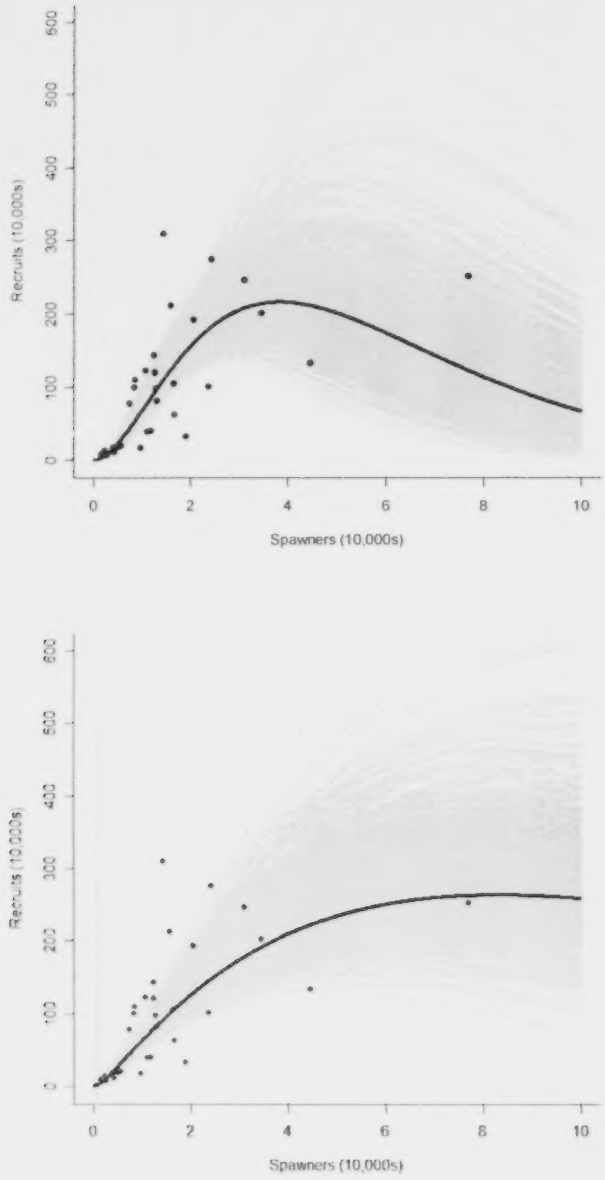

FIGURE 11.
250 random samples of smolt-to-spawner stock-recruitment curves (shaded lines) from the posterior distribution of parameters of the depensatory Ricker model with no prior information (top), and with moderate information on the density dependent term only (μ_β=0.7, σ_β=0.25) only (bottom). The shaded points are the data (subset) and the heavy lines are the most likely models.

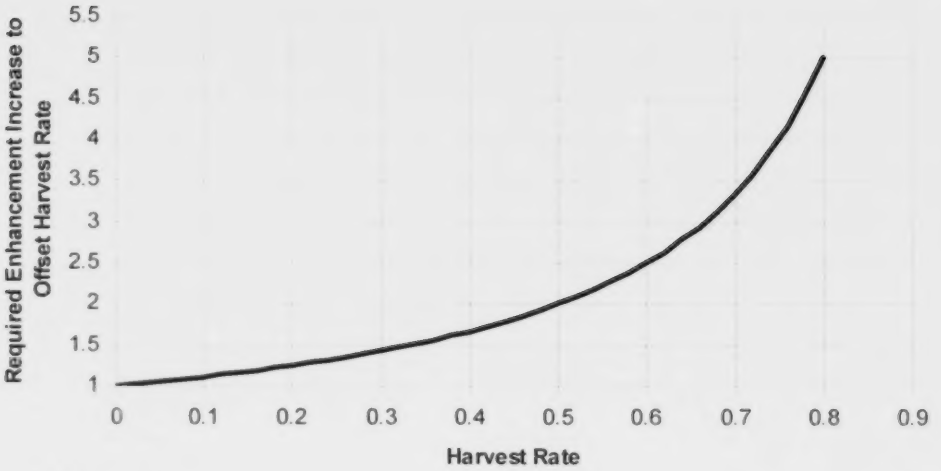

FIGURE 12
Relationship between harvest rate and the required relative increase in the number of smolts per spawner from habitat enhancement (at all stock sizes) to balance the negative effect of harvest on population trajectory (see Eqn. 23).

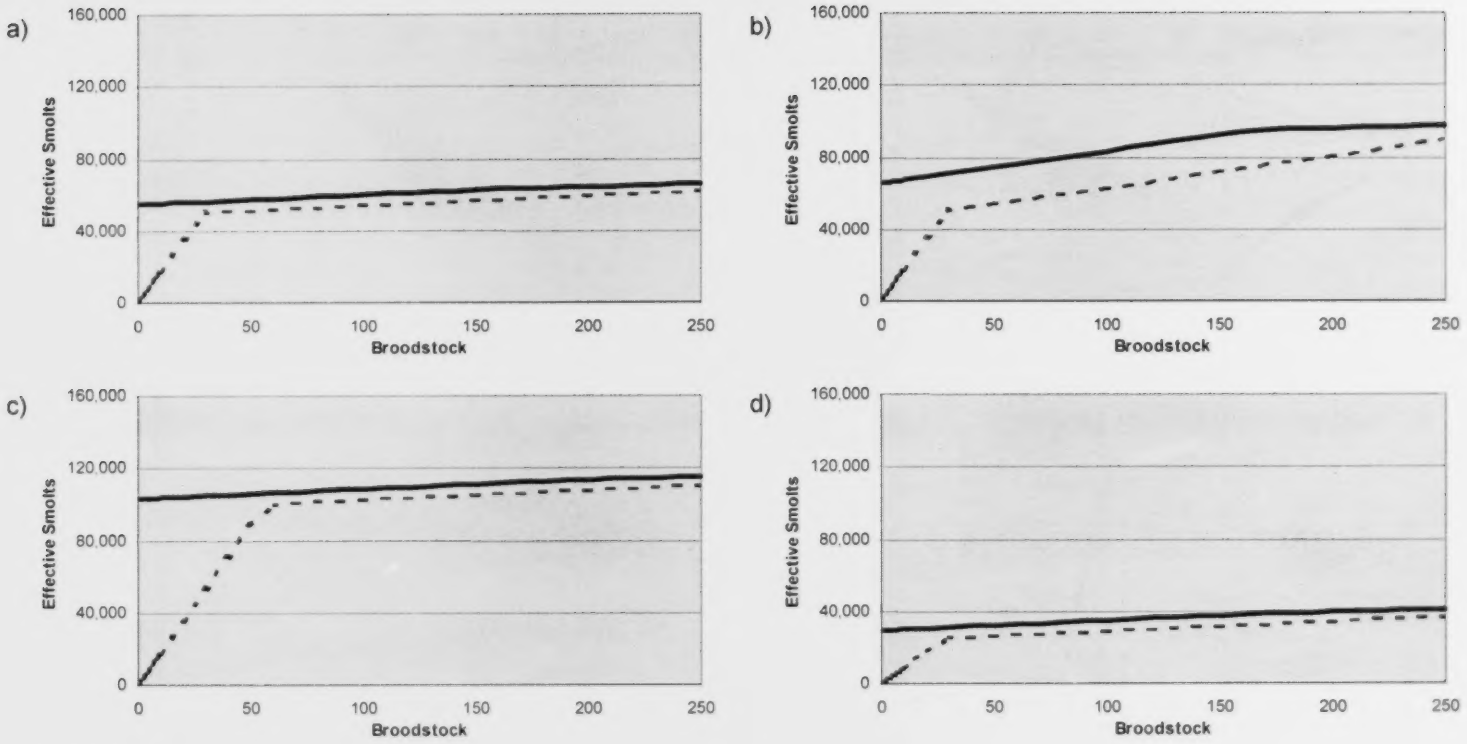

FIGURE 13.
Relationships between the number of broodstock collected and the estimated number of effective smolts migrating past the Sweltzer Ck. fence for captive broodstock (solid lines) and supplementation (dashed lines) programs. a) is based on default hatchery parameters (Table 5). Fed fry to smolt survival in the lake (LKFFSMsurv) was increased by 3-fold from .03 to 0.1 in b). c) is based on default parameters with smolt capacity (SmoltCap) increased to 100,000. d) is based on default parameters with survival of released smolts in the lake reduced from 1.0 (default = release below fence) to 0.5 (release in lake).

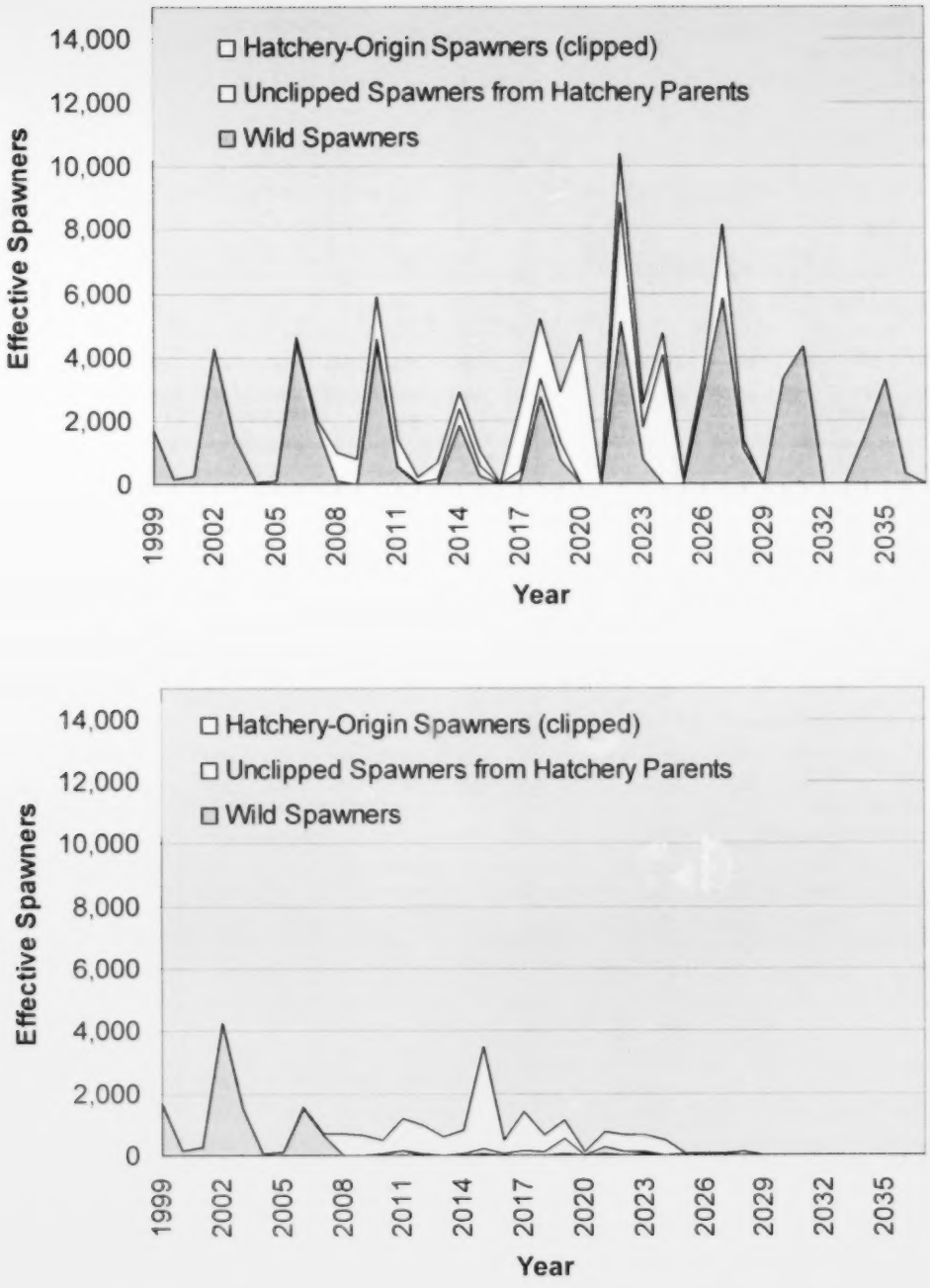

FIGURE 14.
Two realizations under baseline parameter values under a 30% fixed exploitation rate assuming broodstock collection ends in 2007 and no habitat enhancement.

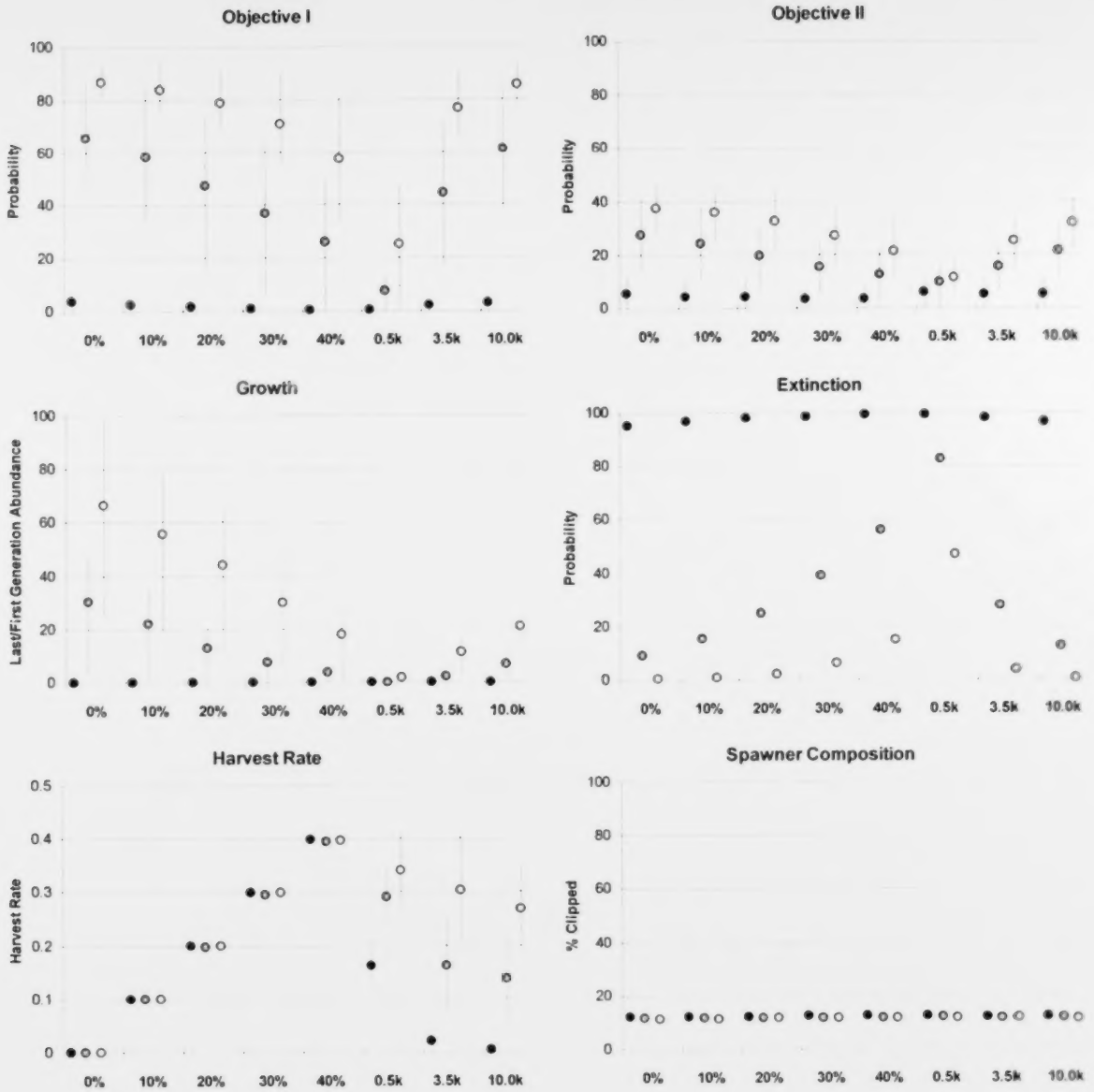

FIGURE 15.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) assuming poor (solid points), average (shaded points), and good (open points) marine survival and pre-spawn mortality rates (see Table 6). The points denote the inter-trial averages and the lines denote the lower 20th and upper 80th percentiles, respectively. Results are based on the default scenario where broodstock collection ends in 2007 and there is no freshwater habitat enhancement. All other model and scenario parameters were set at default values. See Table 2 for definition of performance statistics.

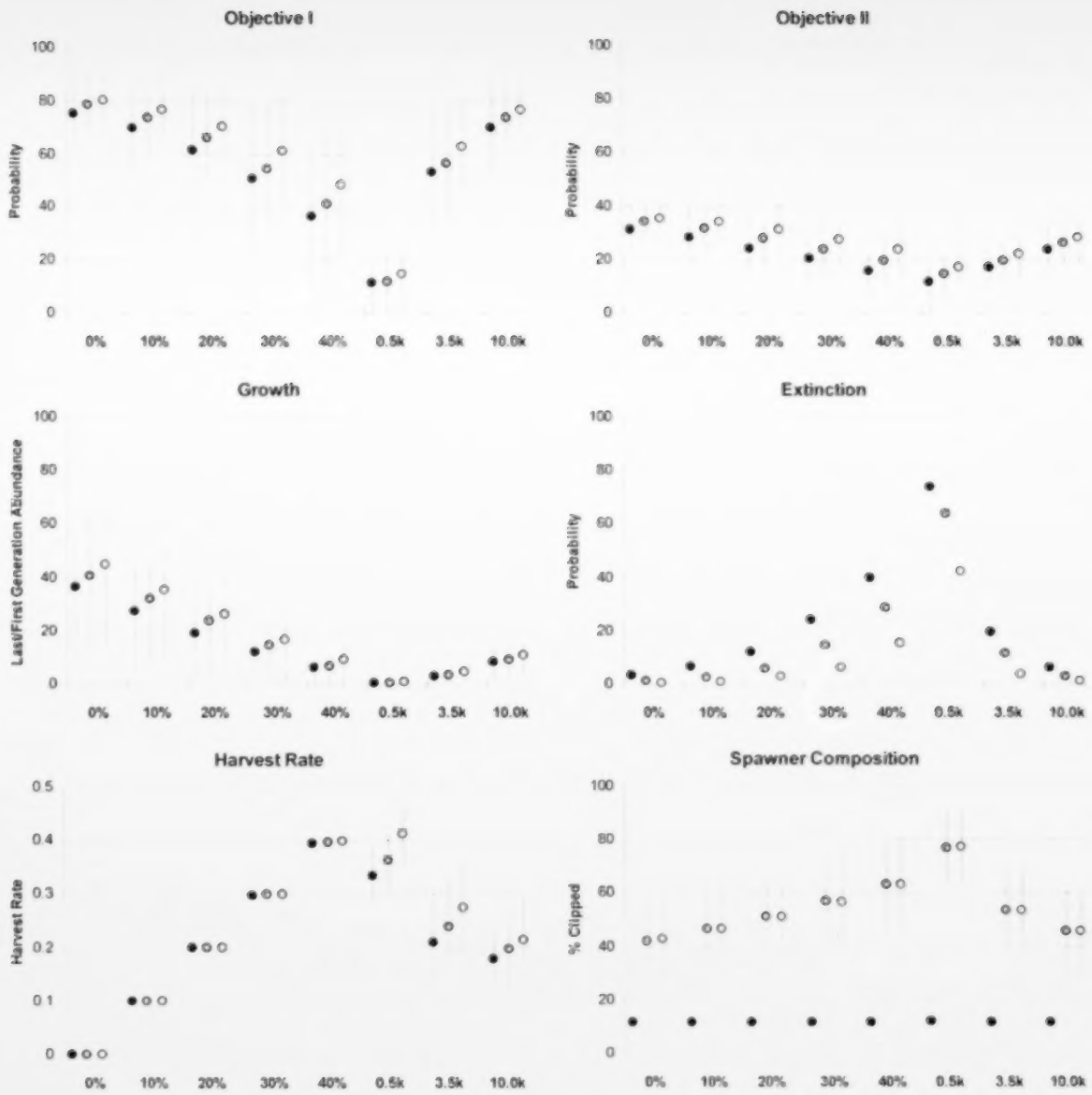

FIGURE 16.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) rules assuming a hatchery capacity of 100,000 smolts with captive broodstock programs ending in 2007 (solid points) and 2015 (open points) as well as a supplementation program ending in 2015 (shaded points). Points denote the inter-trial averages and the lines denote the lower 20th and upper 80th percentiles, respectively. All other model and scenario parameters were set at default values. See Table 2 for definition of performance statistics.

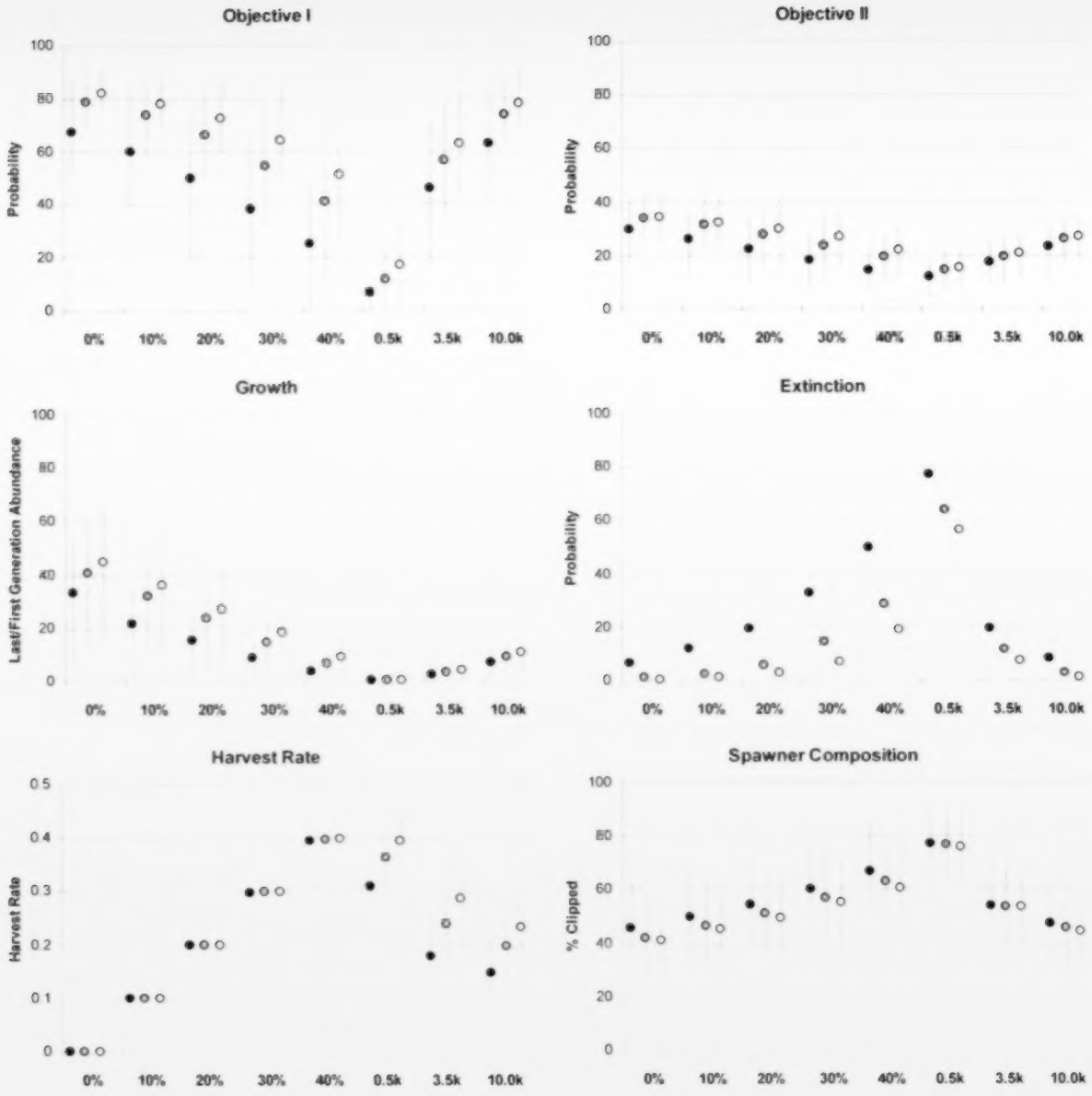

FIGURE 17.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) rules assuming hatchery capacities of 50,000 (solid), 100,000 (shaded) and 150,000 (open) smolts operating as a supplementation program ending in 2015. Points denote the inter-trial averages and the lines denote the lower 20th and upper 80th percentiles, respectively. All other model and scenario parameters were set at default values. See Table 2 for definition of performance statistics.

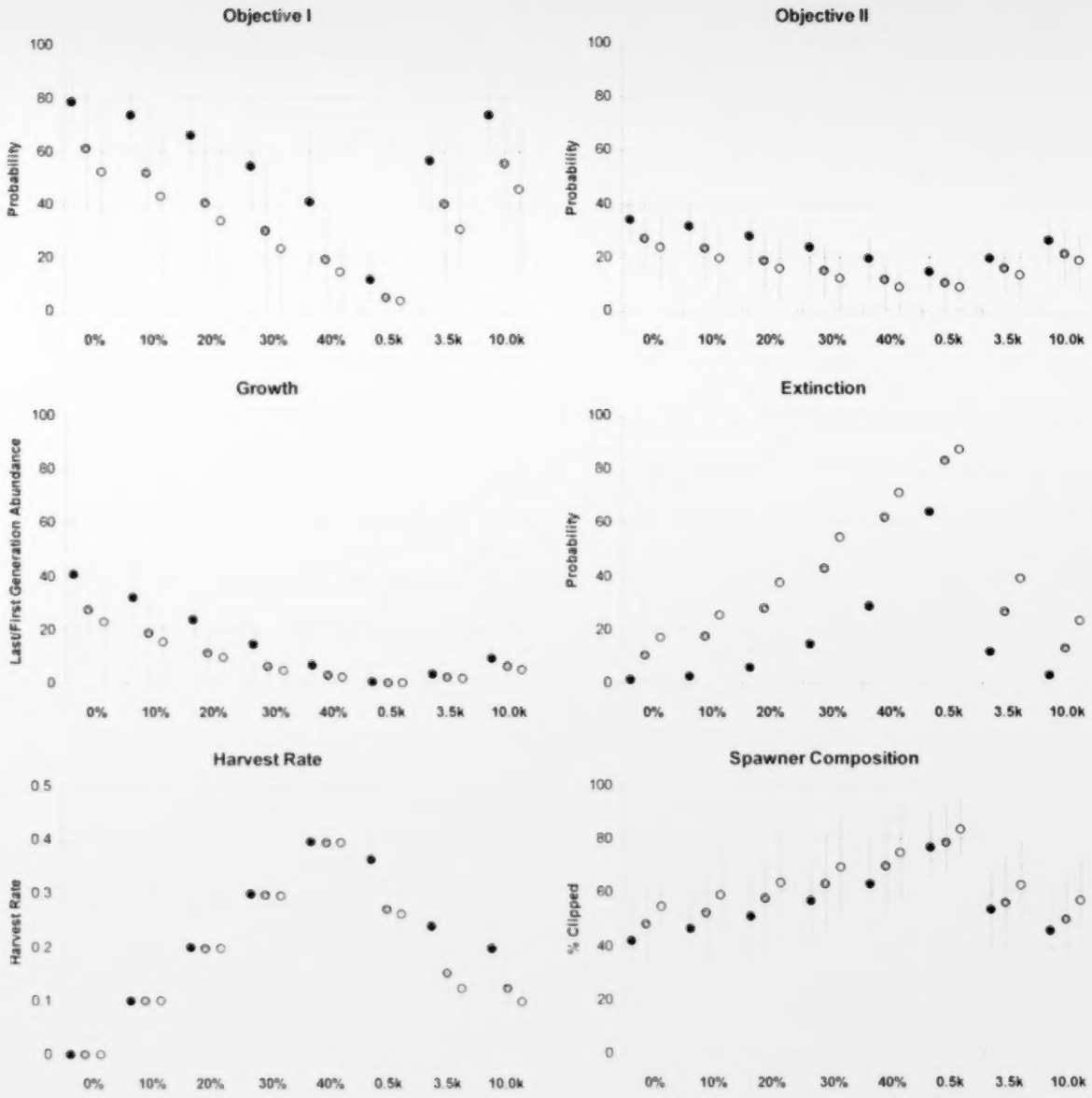

FIGURE 18.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) with a hatchery supplementation program ending in 2015 with a capacity of 100,000 smolts under different assumptions about the relative marine survival of hatchery fish and the reproductive performance of hatchery fish that spawn naturally (solid: Φ_H=0.5 and Φ_U=1; shaded: Φ_H=0.2 and Φ_U=1; open: Φ_H=0.2 and Φ_U=0.5). Points denote the inter-trial averages and the lines denote the lower 20th and upper 80th percentiles, respectively. All other model and scenario parameters were set at default values. See Table 2 for definition of performance statistics.

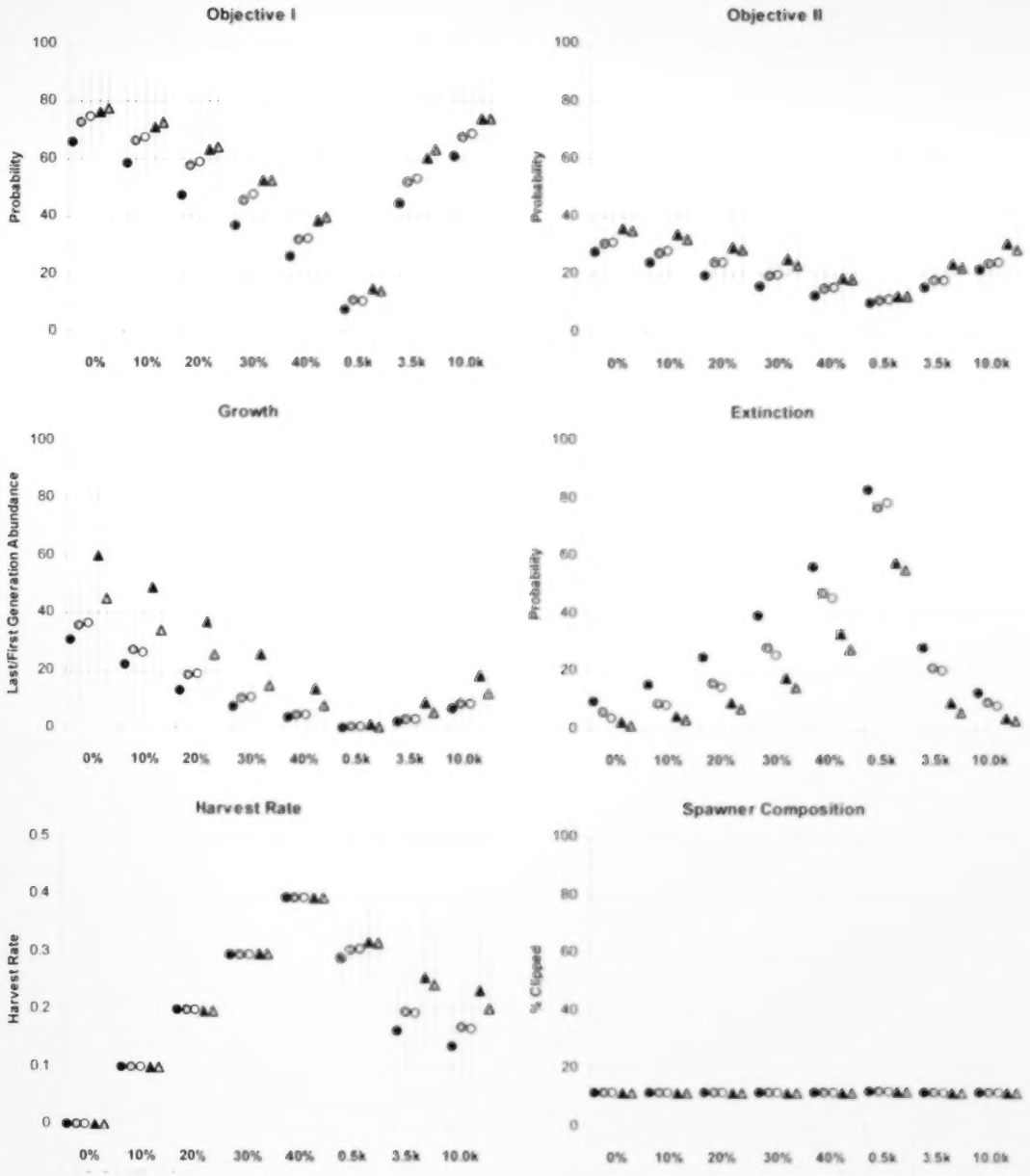

FIGURE 19.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) assuming the current hatchery program ends in 2007 under increasing amounts of freshwater enhancement (solid circle: none; shaded circle: E=1.5, E_d=1, end in 2015; open circle: E=1, E_d=0.5,end in 2015; solid triangle: E=1.5, E_d=1, end in 2035; shaded triangle: E=1, E_d=0.5, end in 2035;) Points denote the inter-trial

averages and the lines denote the lower 20th and upper 80th percentiles, respectively. All other model and scenario parameters were set at default values. See Table 2 for definition of performance statistics.

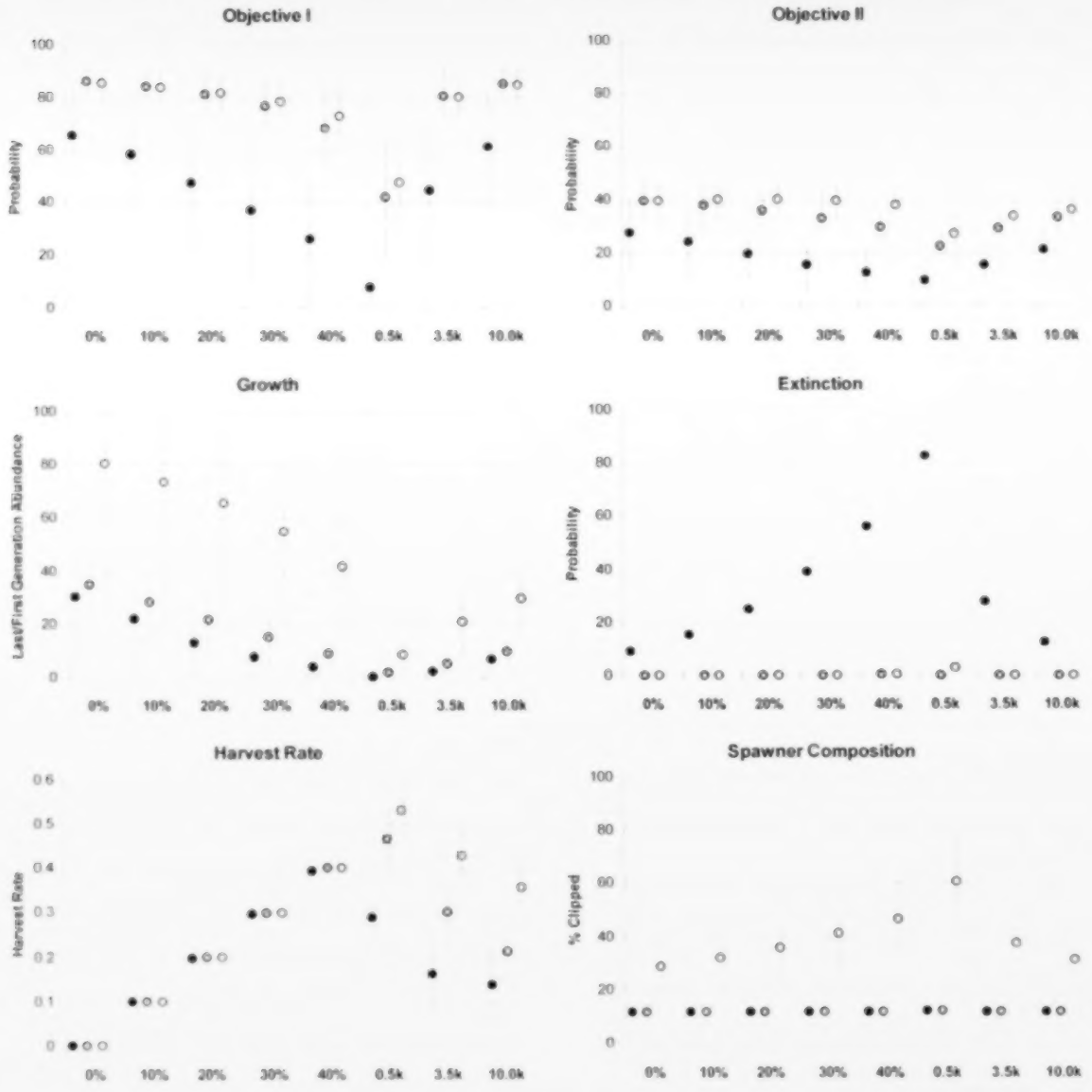

FIGURE 20.
Performance statistics across a range of harvest rate rules (fixed at 0-40% and escapement floors of 0.5-10k) rules assuming base conditions (solid circles, Fig. 15- average survival), base conditions but no-depensation in spawner-to-smolt stock-recruitment (shaded circles), and base conditions with multiple recovery approaches (open circle: supplementation hatchery with 100,000 smolt capacity through 2015, habitat enhancement through 2035 resulting in 50% increase in freshwater productivity and a 50% decline in extent of depensation). The points denote the inter-trial averages and the lines denote the lower 20th and upper 80th percentiles, respectively.

APPENDIX A. SUMMARY OF NATURAL PRODUCTION DATA USED IN MODEL

Table A1. Effective spawners, wild smolts, proportion of adult returns 4 yrs. of age, marine survival rate, and pre-spawn mortality rate, by brood year. The SR removal column denotes which records were excluded for the subset stock-recruitment analysis (n=30). These are years with predator removal, unclipped hatchery production, or years with unknown pre-spawn mortality.

Brood Year	SR Removal	Effective Spawners	Wild Smolts	Proportion Age 4	Marine Survival	Pre-Spawn Mortality
1925		5,065	184,426			
1926	Excluded	2,449	341,428			
1927		76,986	2,522,032			
1928	Excluded	13,693	43,556			
1929	Excluded	4,748	360,860			
1930		7,422	778,822			
1931	Excluded	35,000	1,629,134			
1932	Excluded	2,084	138,733			
1933	Excluded	2,675	309,320			
1934	Excluded	21,426	519,001			
1935		14,327	3,092,446			
1936	Excluded	7,773	1,647,398			
1937	Excluded	1,146	196,393			
1938	Excluded	8,811	1,375,753			
1939	Excluded	66,117	3,976,207			
1940	Excluded	68,683	1,765,430			
1941	Excluded	13,029	705,710			
1942		34,520	2,018,884			
1943		11,042	390,064			
1944						
1945						0.210
1946						0.081
1947						
1948						
1949						
1950						
1951		11,840	395,138	0.973	0.439[1]	
1952		16,656	620,213	0.745	0.071	
1953				0.986		
1954		20,582	1,926,885	0.970	0.033	
1955		24,211	2,752,575	0.996	0.103	

Table A1. Con't.

Brood Year	SR Removal	Effective Spawners	Wild Smolts	Proportion Age 4	Marine Survival	Pre-Spawn Mortality
1956		12,813	976,304	0.971	0.037	
1957		19,030	320,975	0.955	0.088	
1958		12,445	1,429,443	0.977	0.033	
1959		44,626	1,332,280	0.972	0.039	
1960		16,476	1,050,263	0.982	0.022	
1961		12,512	1,200,498	1.000	0.005	
1962				1.000		
1963				0.977		
1964				0.978		
1965		2,293	131,928	1.000	0.155	
1966		15,802	2,118,952	0.989	0.019	
1967		31,007	2,459,276	0.941	0.042	
1968		23,643	1,012,943	1.000	0.044	
1969		5,550	194,867	1.000	0.027	
1970		13,021	817,269	0.997		
1971		8,526	1,092,521	0.993	0.044	
1972		9,682	167,111	1.000	0.182	
1973				0.717		
1974		8,391	998,616	0.937	0.029	
1975		10,600	1,220,908	0.998	0.089	
1976		4,142	167,982	1.000	0.036	
1977				1.000		
1978				1.000		
1979				0.985		
1980				1.000		
1981				1.000		
1982				0.692		
1983				0.993		0.000
1984				0.996		
1985				0.942		
1986				1.000		
1987				0.986		
1988		2,627	65,556	0.852	0.132	
1989	Excluded	572	55,659	0.906	0.210	
1990	Excluded	2,971	183,484	0.906	0.138	
1991				0.958		0.059

Table A1. Con't.

Brood Year	SR Removal	Effective Spawners	Wild Smolts	Proportion Age 4	Marine Survival	Pre-Spawn Mortality
1992				1.000		
1993				1.000		0.000
1994				0.943		0.048
1995				0.964		0.235
1996				1.000		0.656
1997				0.973		
1998				1.000		0.375
1999	Excluded	1,668	62,807		0.046	0.854[2]
2000	Excluded	152	5,746		0.025	0.625[2]
2001	Excluded	255	10,687		0.022	0.000
2002		4,235	110,202			0.131
2003		1,485	80,265			0.234

[1]Outlier removed when summarizing marine survival rates for development of optimistic, average, and pessimistic scenarios.

[2]Estimates based on back-calculation from spawner-to-smolt stock-recruitment relationship.